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A Comparison of North American Small-Mammal Censuses

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Introduction

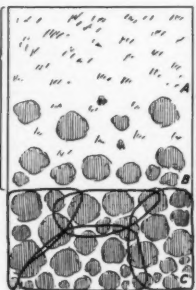
Population studies of mammals commonly fall into two classes: (I) those which concern the total population of a species on all of the ground—but excluding blanks or uninhabited ground—in use during a given period, and (II) those which concern the total population on a given area, much of which is not in use either (a) because it is uninhabitable or (b) because there are not enough individuals to occupy all of it.

Elton, 1932, breaks down population densities of Class I into (1) "economic densities," and (2) "highest densities."

By "economic density" he refers to concentrations of animals on areas embraced by their home ranges or home territories and excluding "blanks" or unused areas, Fig. 1. By "highest density" he refers to aggregations such as groups of ants at rest at night. Concentrations of hibernating bats are another example.

DIVISION OF FIGURES REPRESENTING ANY PART OF THESE AREAS INTO FIGURES REPRESENTING THE POPULATION OF AREA C, YIELDS MINIMUM OR SUBECONOMIC DENSITY DATA FOR THE CENSUS PERIOD

● TREES AND SHRUBS
○ HOME RANGES
◐ UNWOODED AREAS



THIS AREA COMPLETELY AND PLAINLY UNINHABITABLE.

THIS AREA NOT INHABITED ALTHOUGH IT MAY BE INHABITABLE OR APPEAR TO BE INHABITABLE AT THE TIME OF THE CENSUS. USE OF THIS EVEN IN PART MAY RESULT IN A PSEUDO-ECONOMIC CALCULATION

THIS AREA ENTIRELY COVERED BY HOME RANGES OF GRAY SQUIRRELS HENCE COMPLETELY INHABITED

DIVISION OF THE POPULATION FIGURE BY THIS AREAL FIGURE YIELDS ECONOMIC DENSITY DATA FOR THE CENSUS PERIOD.

Fig 1. Diagram illustrating economic and subeconomic densities of mammals with gray squirrel as example.

He calls population densities of class II, "minimum densities" and Leopold, 1933, attributing the term to Elton, calls them "lowest densities." They may also be called subeconomic densities or non-economic densities.

Most mammalogists in the past have apparently assumed that they were

making studies of economic densities, but many have failed to achieve this aim, either because they failed to recognize the relation of time to the results they obtained, or because they failed to recognize the nature of a species' use or non-use of the area censused. They failed to recognize blanks.

Most obvious sign of this failure is that many authors do not state whether their figures apply to the annual low population immediately before birth of the first young of a season; or the annual high, usually when the last broods of a season are being born; or the population at some time between these two events.

Most authors who follow an elaborate census technique do, however, state the length of the census period upon which they based their figures. Dalke, 1938, studying cottontails; Burt, 1940, studying various small mammals followed by Blair, 1940, studying prairie deer mice and meadow mice have plotted the distribution of individuals on maps during census periods of stated lengths and stated times of the year, thus recognizing the time factor specifically as well as the difficulty of recognizing blanks or unused territory without some such special device as mapping.

Dalke further recognized the fact that the longer a census were extended, the more ground an animal might have covered by writing of a "seasonal range." Blair wrote of a "monthly home range." One might similarly write of daily, weekly, monthly, and yearly populations, densities and ranges, thus standardizing future observations.

The present paper is written in the attempt to compare those population studies which may be, or were intended to be, studies of economic densities, in such a way as to show how much and why they deviate from a standard, and also to derive some common denominator from them. This, confessedly, is a large order, but there are a surprising number of interesting censuses and near-censuses, many scattered in general papers, which may well be compared and which throw useful light upon the subject of mammalian abundance.

In order to convert animal populations to a common denominator, Elton, 1932, calculated weights of economic densities of ants and men, and found their weights approximately alike per acre. A similar concept had common use among early German foresters when calculating the number of deer which could be supported in a given acreage of forest, according to Clepper, 1931, and others. Experience had shown them that one red deer, a large species, was the equal of two smaller fallow deer or four of the only small roe deer. Their experience found further extensive use on western ranges in America where horses were found roughly equivalent to cattle, and each of these the equivalent of five goats or sheep when calculating the amount of stock which a given acreage of range or pasture might support.

This general method is here extended to compare populations of various kinds of smaller mammals. Average adult male and female weights in grams are used to measure the size of individuals or the various kinds, and a comparative weight factor is derived by multiplying the population per acre by this weight. One may also derive home range factors by dividing individual

weights by home range areas. This gives a common denominator for comparing results of various kinds of censuses. It may be added that conclusions drawn in this paper will fall well inside the limitation of the method.

Comparison of Censuses and Data

Carnivorous, Omnivorous and Insectivorous Species

OPOSSUM, *Didelphis virginiana* Kerr.—Although not attempting a thorough census of the opossum, Yeager, 1937, furnished some figures which reveal the approximate population levels of this omnivorous species. While trapping for fur on an eighty acre farm in Mississippi, he caught an average of one opossum per three acres during a relatively long period from November 15 to January 1. No migration, he felt assured, occurred from outside of the area in spite of the long season, because he also trapped up and down a creek which flowed lengthwise through the farm, thus cutting off the principal migration route. Although some of the area was farmed and the woods lightly pastured, good den trees were numerous and the entire farm averaged out as good opossum habitat because of interspersed woods and creek bottom with the open fields. Therefore the factors derived below are economic or nearly economic factors. Yeager's theoretical calculations showed that, at the height of the annual population, which is slightly before the trapping season, there might be one opossum per two acres on such an area.

They averaged about 5.5 pounds each. Adapted in terms of grams to populations discussed above, this method gives weight factors in excess of 830 to 1250 per acre on this area, practically all of which appears to have been in use and at a time of the year when the population was at or near its peak.

HAIRY TAILED MOLE, *Parascalops breweri* (Bachman). — Bole, 1939, censused hairy tailed moles.

He used ordinary mouse or death traps, set in the moles' burrows, and recorded three-day populations varying from one to twenty-four hairy tailed moles per acre, but most often around four. Taken at their face value, they indicate three day factors varying from 50 through 205 and up to 1225, since adults of this species weigh about 50.5 grams in the region censused. The higher figure may have been due to drift while the census was progressing. The factor 204 is most frequent.

Eadie, 1939, discussing population density of this species in New Hampshire, found an average of 1.2 moles per acre while death-trapping an area of "approximately 27 acres of varied topography" about one-fourth of which he stated was unsuitable for mole habitation. Having conducted his census "for a period extending from August, 1935, to June, 1936," omitting January and February; not having taken all the animals; and admitting influx, his census is not subject to comparison, the figure of 1.2 moles probably representing a subeconomic density.

STAR-NOSED MOLE, *Condylura cristata* (Linnaeus).—Six per acre was the

highest three day concentration of star-nosed moles recorded by Bole, 1939. At 51.8 grams per mole, this represents a factor of about 310 per acre.

Hamilton, 1931, wrote that there were "probably fifty" star-nosed moles living in an area of about three acres near Cayuga Lake, New York. He remarked that they were outranked in number by both *Blarina* and *Peromyscus*. "It is probable," he added, "from field observations and intensive collecting, that there must be an average of five pairs to the acre scattered through the area of swamp land that borders the lake for nearly a mile."

Hamilton found the average size of the star-nosed mole to be about 52 grams, indicating factors of from 520 to 880. This estimate was instantaneous or "photographic" in nature. Most such estimates appear to be based upon populations of breeding pairs, hence are probably intended to be yearlong economic figures.

MASKED AND SMOKY SHREWS, *Sorex cinereus* Kerr and *Sorex fumeus* Miller.—Townsend, 1935, conducted an elaborate deathtrap census of masked shrews and smoky shrews, both extremely small insectivorous mammals, from "early June to late August" in an attempt to discover their population densities in various types of habitats.

The details of his census methods were complicated, but the principle relatively simple. His object was to catch all of the mice and shrews on a given area, but no more, thus to discover the size of the populations. For this purpose, he used the familiar mouse traps, set in groups of threes, one baited with bacon rind, one with salted peanut, and the third with a raisin, the object being to present baits desirable to creatures of widely differing food habits. Details omitted, the method consisted essentially of getting an entire area, amounting to one-tenth of an acre, and only about three rods wide, trapped in two weeks' time, by moving three two-rod rows of 99 traps progressively over it.

When he began this method of censusing, Townsend evidently felt that very few shrews would migrate onto his area while the census was being made, but it soon became evident that this was not the case. Casting about for a solution, he noted that each time he moved a row of traps forward, he would catch numbers of shrews for three nights, after which the catch would decrease suddenly. He then assumed that the first three nights' catch was of shrews which lived on the area and that any caught later were migrating from elsewhere.

These methods led Townsend to believe that *S. cinereus* and *S. fumeus* together reached populations varying from 0 to 63 per acre, but he added, "It is noteworthy that the estimates for *Sorex* (as a group) in woods habitats are usually around 11 or more per acre if this genus is represented at all." In view of the fact that females are generally less prone to migrate than males, it is interesting to note that when Townsend's tables show a population of 15 or less per acre, at least half are generally females, but where he lists higher figures the larger proportions are generally males; indicating that considerable migration might have taken place to produce the higher figures. Unfortunately the exact significance of these numbers cannot be judged because his census

units were about one-tenth of an acre, so that when he caught one shrew in a set, it would automatically indicate 10 per acre by his method of calculation. This would happen often.

Bole, 1939; Burt, 1940; and Blair, 1940, criticized Townsend's procedure, pointing out that trapping only one-tenth of an acre, even for a few days, permitted much migration onto it, and that prolonging the trapping on such a small area for two weeks introduced an intolerable amount of error. By trapping areas of varying size, Bole showed that the larger the area trapped the smaller was the catch, due to progressive reduction of migration.

Since masked and smoky shrews differ so widely in weight one cannot derive correct factors without knowing actual numbers of each. The above population data would indicate per-acre factors varying from 0 to at least an excess of 260 because the smallest shrew of the two here discussed weighs about 4.13 g.

These factors are of interest because of their relation to Bole's (1939) census of the same species.

Bole tried census areas varying in size from one-tenth to about half an acre, the areas being either square or circular in outline so as to reduce the relative amount of margin which, in turn, cut down the amount of drift into his census areas. Instead of setting his traps in lines or grid as Townsend did, Bole set his traps at the entrance to all burrows and in all runways which he could find on his census area, using only as many traps as needed for the purpose. At least 100 were found necessary in each half acre quadrat. He used rolled oats or dried fruit as bait, except during the rainiest weather which made them soggy, but felt that he captured the moles and shrews as efficiently without bait as with, because of having placed his traps in runways or at burrow entrances. Like Townsend, he found a sudden drop in numbers caught after the third night and therefore considered the first three nights' catch only as being of animals living on the census area.

He discusses data from the 150 foot square (half-acre) areas with three day trapping periods as being sufficiently free from drift or migration to nearly represent the actual populations of animals.

MASKED SHREW, *Sorex cinereus* Kerr.—Bole's estimates of numbers of masked shrew vary from 0 to 11 per acre, but the number of observations is limited. A concentration of as many as 5 per acre he attributed to flooding of habitat causing a temporary concentration on nearby unflooded areas. The shrew averages about 4.13 gms.

Factors of 20 to 45 based on these figures fall within those derived from Townsend's extremes and lie close to those derived from his most frequent population estimates, namely 11. Bole's estimates, being aimed at discovering how widely distributed the animals were, included many blanks. He did not state at all at what times of the year they were made. His lowest figures are undoubtedly in the nature of subeconomic densities with no clues to where economic levels begin.

SMOKY SHREW, *Sorex fumeus* Miller.—Bole's estimates of smoky shrew numbers varied from 0 to 58 per acre, but most of the figures listed in his tables fall between 5 and 10, hence do not differ essentially from Townsend's figures for mixed populations of smoky and masked shrews. The average weight of adult smoky shrews being about 8.14 grams, three-day per-acre factors up to 470 are indicated for this species.

Hamilton, 1940, trapped various habitats in New York during July and August to determine population levels. His method was similar to that of Bole. In the more favorable habitats of beech and hemlock he established several quadrats 100 by 100 feet, which encompassed 0.23 acre, placing 300 traps in the most promising runways. He visited these traps at dusk and dawn for a three-day period or "until the catch had been so reduced it was assumed the major part of the population had been removed." On one quadrat he caught 12 smoky shrews by this method; on another, 10; and on the third, six. "Thus, on three quadrats of nearly a quarter acre each," he wrote, "there were collected 12, 10, and 6 smoky shrews, or an assumed average population of between 25 to 50 per acre."

In 1936 several quadrats on which he collected "produced an estimated population of 9 and 14 per acre." He believed that on some other quadrats on which he trapped the numbers might not have exceeded 5 or 6 to the acre.

Per-acre factors, based on his figures, range as follows: 400, 200, 114, 73, 41. The entire range from figures by all authors is 20 to 470.

Even the highest factors derived for masked and smoky shrews above were only about half as great as the lowest for opossums and raccoons. If considerable drift of shrews had occurred, as is possible on such small census areas, their true numbers and factors would not even reach so high.

OLDFIELD SHREW, *Cryptotis parva* (Say).—Wooster, 1939, censused oldfield shrews, in an attempt to discover the animal composition of a Kansas prairie, the purpose of his census being such as to include more blanks than used territory, hence not subject to treatment or comparison here. He estimated 614 on 640 acres, or less than one per acre. No trapping dates were recorded.

MOLE SHREW, *Blarina brevicauda* (Say).—Several authors have made estimates plainly as to economic densities of the mole shrew. Shull, 1907, estimated four mole shrews per acre of swamp in southern Michigan; Seton, 1909, estimated 50 per acre in a moist woodland in Connecticut; and Hamilton, 1931, estimated eight to the acre of choice locality. Williams, 1936, estimated as many as 299 per acre, but he used quadrats only 32.75 feet square and confessed that the error due to migration was so great that he had no way of deriving a population figure anywhere nearly approximating correctness. As will be seen later, populations of this species over 25 per acre are probably aggregations or due to drift during census.

Townsend and Bole, using the same methods as for smoky and masked shrews, estimated mole shrew populations as high as 104 and 48 per acre

respectively. Their estimates probably were of numbers at some point between their annual high and annual low points, although they gave no definite dates. Both had trapped blanks to varying extent, and both had to contend with drift into their small census areas.

Wooster, 1939, found 337 per square mile, but most of the area he trapped was blank at the time.

Blair, 1940, used a live trapping-marking-release method developed by Burt and found monthly populations of from 0.8 in late August to 2.2 individuals per acre in late September, but he had also trapped extensive blank areas and used these in calculating abundance even in his highest figure. "In no month," he wrote, "was the entire area of the plot covered by the ranges of the shrews."

He determined the home ranges of 23 individuals, the average being 0.4 acre which agrees with Burt's finding. Theoretically, one might get an economic density of as little as 2.5 mole shrews per acre from Bole's home range figures, but actually the home ranges overlap to such an extent that economic densities are in excess of this figure. Per-acre factors are accordingly above 50 in regions where the densities were studied and where mole shrew adults appear to average about 20 grams each.

Just how much home ranges and home territories of this and other mammals vary under varying food and cover conditions is unknown. Where food is scarce mammals must generally require measurably larger home ranges and territories than where food is abundant. There is, however, a limit to their endurance in the matter of covering ground while garnering the necessary materials for living, and generally where they cover large linear distances the lateral distances are correspondingly narrow. As a result, each species has a measurable characteristic home range or home territory. This may to some extent be used to discover populations beneath which average members of the species fail to maintain themselves.

Burt, 1940, studied populations of mole-shrews by means of a live trapping technique by which he not only enumerated the number of shrews in a given area, but also the amount of that area being used by them during the census period. Box traps made of half inch boards and provided with food and cotton were set in rows in the area to be censused, ten yards between traps having been found most satisfactory for shrews. When caught the animals were marked and released and the place of capture recorded. The released animals tended to maintain their home territories and prevent migration into the territory. By catching these individuals frequently, Burt was able to outline the territory they were using. Although his methods were refined and used chiefly for woodland deer mice, he caught 16 mole-shrews more than once and many of them six times. "The normal home range," he concluded, "is probably about fifty yards in diameter and covers about 0.4 acre. If the animals maintain territories during the breeding season, the breeding population should be no more than about five per acre, and the maximum population, including breeding adults and young, should be about twenty-five

animals per acre. . . ." This high figure would be attained only if the entire population remained stationary. This did not happen in the case of woodland deer mice studied by Burt and probably does not often happen in the case of mole shrews. In the case of deer mice only one-third the possible high figure was realized.

Adult shrews in Michigan averaging about 20 grams apiece, give theoretical factors of from 100 to 500 per acre. One-third of the mole shrew population calculated by Burt would amount to only eight individuals per acre or a factor of about 160.

No doubt, populations many times higher than 25 per acre do frequently occur, but for how long has not been determined. Bole, as has been noted, estimated a three day population, season unstated, on a half acre square as high as 58 per acre. Dice, 1938, however, suggested that if the habitat is uniform beyond the outside line of traps on areas censused after Bole's manner, the area from which the animals come will be not only that on which the traps are set but will include an additional strip about one-half the mean width of home ranges of male and females combined. Burt found that the average distances over which mole shrews ranged was 153 feet. If applicable to Bole's figures, it indicates that the 58 shrews came not from half an acre but from 2.1 acres making the population about 27 per acre, hence tending to confirm Burt's calculation of a ceiling of about 25 mole-shrews per acre, and a factor of about 540, provided all shrews remained where born.

No other high census figures were obtained or reported in such a way as to be subject to Dice's adaptation of figures. One may object that since Bole set traps in runways and at burrow entrances, leaving his traps only 3 days, he did not catch a considerable number of animals from outside his census area and that therefore his figures are essentially correct. This is perhaps true; the point having yet to be proven. Most of Bole's censuses, however, fall below 25 per acre and, since migration is smallest when the shrews are least abundant, we may accept the lower figures as most reliable. This tends to indicate that populations higher than 25 and factors higher than 500 are in the nature of aggregations or due to drift.

RACCOON, *Procyon lotor* (Linnaeus).—Yeager caught nine raccoons, an omnivorous species, on the same area during similar circumstances as opossums, and calculated the total population at 13. Adults average about 16 pounds, and the per-acre factor for them varied from 810 to 980 while populations were at and near the maximum annual population. The farm upon which he trapped apparently averaged out as good raccoon habitat without large blanks.

LONG TAILED WEASEL, *Mustela frenata* Lichtenstein.—Seton ventured that "a pair of long-tailed weasels to every square mile of prairie would represent the utmost of this species in Manitoba during primitive times." In so doing, he was undoubtedly thinking of breeding pairs on areas most of which were suitable as weasel habitat. Desiring to give a picture of the prairie as a

whole, he did not describe how much of this habitat was in actual use, hence the density stated is probably subeconomic. Conversion of his figure, however, makes clear how populations of predators which do not depend largely on insects as food, compare with omnivorous and insectivorous species. Adults in Manitoba weighing approximately 250 grams, the per-acre factor is almost 1.0.

Seton also calculated the possible number of weasels per square mile in Pennsylvania, basing his calculations on an involved series of figures on reproduction rate, number of weasels caught, etc. His resulting estimate was five per square mile. Not a census, in the proper use of the term, and subject to much doubt the figure is significant in being low.

Yeager, 1937, basing his estimate of weasel populations on the same trapping methods and calculations used for opossums and raccoons, set the population density figure on an eighty acre farm in Mississippi at 0.3, or a rate of 2.4 per square mile, probably having the early winter trapping season in mind as a point of time.

Errington, 1938, wrote, "Snow trails of weasels often indicate densities of one or two per square mile."

Errington's study was intended to give a general picture of the weasel population of a large area, mainly farmland of which little was used by weasels either because some was barren or because there were not enough weasels to cover all of it, or both. The factor derived from his study varies from 0.5 to 1.0 and is subeconomic in nature.

A more detailed use study on a similar area follows:

Polderboer, Kuhn and Hendrickson, 1941, found five long-tailed weasels on a 160 acre farm by following all trails made in snow during single nights over a period of several winter months. The average distance traveled by these weasels in one night was about 25 rods, and the maximum was 45 rods. They rarely departed from the central den more than 18 rods in any direction. After finding the general range of an individual, it was usually a rather simple matter to relocate the animal on subsequent visits because each tended to stay within a relatively small area. Two weasels occupied a 5.5 acre weed patch during the winter and spring of 1939. A single individual lived in a 10 acre patch of oat stubble and two others, one a least weasel according to Polderboer, 1941, were found in a 28 acre field of sweet clover. Only 43 of the 160 acres were therefore occupied during the spring and winter months and, during the months observed, even this 43 acres was not completely in use.

The general purpose of the census appears to have been to discover the abundance of weasels on a 160-acre area of farmland typical of the region covered by the Wisconsin glaciation. As such a census, it was not designed to result in a study of economic density. Perhaps, by their general nature, the detailed censuses may also not have been intended as economic density studies. They do, however, come close to being in the nature of economic censuses, and we may therefore examine factors derived from them as helpful in interpreting densities. The long-tailed weasels in this region appear to average

about 165 gms. The per acre factors for two long-tailed weasels on 5.5 acres is 60. For one on ten acres it is about 15. If, as stated above, the long-tailed individuals do not leave their central dens by more than 18 rods in any direction, they used only 31,416 square yards or 6.5 acres of this entire field during the months under watch. This home range density indicates a home range factor not smaller than 25 during an indefinite period covering a number of winter and spring months.

MINK, *Mustela vison* Schreber.—Guthrie, 1925, estimated one mink to approximately 2.5 square miles on twenty-two National Forests in Oregon and Washington. The estimate, being intended to take stock of this animal over wide and varied areas, plainly furnishes only minimum density data. Seton, 1929, guessed the number of minks in Manitoba at a pair to every square mile without indicating whether he was thinking of high fall or low summer densities.

Marshall, 1936, made a most serious attempt to census this important species.

Trying various means of discovering how many individuals were using his census area, he rejected trapping and marking the population, and making den and feces counts as either too indirect or too difficult. The study soon showed that tracking in snow might give valuable data and suggested the feasibility of developing a census method by tracking during the winter months. Examination of mink tracks, live specimens and museum records showed that in southern Michigan, where Marshall carried out his study, hind foot tracks less than 2.75 cm. long were made by female minks and those greater than that were made by males during the period between December and March. Provided with this information, Marshall used every snowfall as an opportunity to track and outline the home ranges of males and females as much as possible. In this, he was most successful in discovering the ranges of females because their wanderings were neither so extensive nor as involved as that of males. The females tended to remain in areas of approximately 20 acres while the males wandered so extensively that the size of their territories was too large to be estimated with accuracy from the data at hand. However, on the three square miles censused, he found the home ranges of five females and the tracks of five males or a population of between three and four minks per square mile. Marshall added that this was the population following a heavy trapping and hunting season, and because the home range maps and other data supplied by him showed that the minks were using only a limited amount of the territory, we may note that his figures are minimum density figures.

Fortunately his map gives a clue as to possible economic density of minks. It shows that of two square miles occupied by four minks only about seventy-two acres were encompassed by their wanderings after a snowfall in February. At 908 gms. per mink this gives a single-day economic factor of 50. This factor is similar to the largest factor of 60 derived for long-tailed weasels. It is quite likely that the amount of territory encompassed in several months

would be larger and the economic factor correspondingly smaller, but the fact that minks confined their wanderings to the area around the stream indicates that it would not differ greatly unless, having "hunted out" the prey species in the area occupied during the winter, the mink population shifted to another area not previously occupied. That this may happen is indicated by Seton's comment that the mink's habit seems to be similar to that of weasels in that it hunts a given area until the game grows scarce either through death or flight, after which it moves a mile or two in search for new hunting grounds. Seton states further that this may happen several times a season.

OTTER, *Lutra canadensis* Schreber. — All otter population figures with which the writer is acquainted represent subeconomic densities. None can perhaps be classed as censuses, certainly not economic densities. Heaviest densities are those mentioned by Seton, 1929, of one otter to eight square miles in Ontario, but even these include extensive blanks in the shape of dry land which, except for a narrow strip of shore, is practically of no value to otters. Their hunting grounds are chiefly part, not always all, of the waters in and near which they live. One may well doubt that densities of otters fall below several to the square mile of water surface and nearby shore where the entire body of water is used for hunting.

SKUNK, *Mephitis mephitis* Schreber.—Seton, 1929, making a guess based on general experience, stated, "There are many parts of the range where one skunk per square mile is quite a likely rate," but, in doing so, he apparently was not thinking of an economic density.

Edge, 1935, using a method of determining animal populations consisting of "a combination of trapping, observation and den counts" came to the conclusion that skunk populations in certain areas in western Oregon varied from six to thirty-two per square mile, presumably breeding pairs, near the beginning of the breeding season.

Hamilton, 1936, stated, "In the hundred acre Cornell University orchard during the springs of 1933 and 1934, there were estimated to have been approximately 8 or 10 skunks." These figures amount to about one skunk to 10 or 12 acres.

Since skunks vary considerably in weight between early winter when returning to their dens and later winter when leaving them, it is necessary to strike some average measure of their size. Five pounds and ten ounces, or 2586 grams appears to be substantially correct for the areas where populations were measured.

Seton's population figures, therefore, indicates a per-acre factor of 4; Edge's indicate from 25 to 130, and Hamilton's indicate factors of from 208 to 255.

Allen, 1937, 1938, and 1939, caught skunks in live traps and marked them during their least mobile period in Michigan from September 17 until March 22, releasing them to be caught again. By this means he gained data as to which skunks were resident on the area and which merely crossed it,

remaining only a short time. He supplemented these observations by digging out skunks from dens in which he felt, after watching tracks, there might be a large number not marked by trapping. By this means he marked 23 resident females and 39 males, of which he concluded only 23 were resident, since the sex ratio appeared to be 1 to 1. This made a total of 46 skunks using a 500 acre tract, giving a density, probably economic, of 1 skunk to 11 acres. This figure falls exactly between those quoted by Hamilton and has every indication of being an economic density for, according to Allen, "Although we know very little of ordinary population densities it may safely be said that this represents a heavy concentration of these animals." The factor for this figure is 230.

Jones, 1939, wrote, "In Delaware County, Pennsylvania, the autumn peak population density is 31 per square mile, which indicates about 21 acres per individual when perhaps most of the square mile is in use by the numerous population." His method of estimating the population consisted of trapping and a limited amount of snow-trailing on a farming area of about $1\frac{1}{8}$ square miles, half of which was cornfield, wheatfield, and pasture; and about half of which was rolling grassy hills, brushy fencerows, wooded ravines and hollows ideal for skunks. His census was, however, a three-year one, hence appears to have included most of the individuals that lived and died on the area during the periods beginning with the winter of 1936-37 and ending with the winter of 1937-38. If so, the population at any one moment must have been considerably lower than 31, how much lower being impossible to tell. The latter figure is similar to that derived from Edge's estimate of 32 per square mile in Oregon, quoted above. It is not strictly comparable with others because of the great duration of the census period.

Scott and Selko, 1939, like Jones, also attempted to census these animals in a mixed countryside, thus obtaining a subeconomic density figure typical of certain sections of farming land in Iowa. Their figures accordingly vary with the number and size of blanks included in the census. They combined 128 square miles of countryside, examining every cutbank, woodland, hedgerow and brush patch which experience told them might shelter skunk burrows. By this means, they found 37 families of skunks on 64 square miles of land in Boone County, and, finding the average family consisted of 7 individuals, calculated 4 animals to the square mile.

The highest single concentration was one of 8 families on half a section or one skunk to 7 acres which was undoubtedly an economic density. The per acre factor for this population is 285. This is the highest so far derived for skunks.

In another county, they found only 1.64 skunks per section, where the highest density was 6 families on one section, or one individual to every 15 acres. This yields a factor of 170. The small figure undoubtedly represented a subeconomic density; the large figure, probably an economic density.

All of the authors who made any organized attempt to census skunks hit upon densities of one skunk to from 10 to 20 acres, most of the figures being

nearest 10 to 12, and to judge from the description of the area censused, representing moderate to high economic densities.

None, because of the requirements of their problems, attempted to find just how much of the area censused was in use, or to discover what a low economic density might be, although when describing the area censused, Hamilton and Allen indicated it might all have been in use. It may be that one skunk to from 10 to 12 acres is usually an economic density, but not a high one.

Some light is shed on this problem by a knowledge of the home range of skunks. Seton, 1929, states that the home range of each individual is very small and that he has often followed its tracks in the early or late snow from its den through its hunting expedition and return to its den. At no time did skunks go more than 200 or 300 yards from home. Even during warm weather, when skunks are more active, Seton believed average individuals would not wander farther because of corresponding ease with which they might find food. Mills, 1900, stated that the territory over which skunks ramble for food or amusement is about 1000 feet in diameter. These data indicate that the average skunk might confine his wanderings to from 7 to 18 acres and that, because home ranges overlap, economic densities must at least be at a rate which would allow less than 18 acres per skunk and possibly less than 17 if the habitat were rich in food and other requirements. This indicates further that Hamilton's and Allen's figures represent economic densities.

Having so far discussed populations, and factors derived from them, for two species of omnivorous animals and a group of insectivorous species from moles and shrews through skunks, we may here pause to see how they compare.

Home range factors indicate that mole shrews are not likely ever to become so uncommon as to have an economic factor as low as 34. Actual studies by Burt, indicate that they may rarely go so high as to have an economic factor of more than 557. Thirty-four is the factor derived most frequently from Blair's figures. The highest factors for masked and smoky shrews, derived from Bole and Townsend, is 250 or somewhat less than half of the highest theoretical factor derived from Burt's studies. Only under circumstances obviously subject to drift or due to guess (Seton, Boles, and Townsend) does the factor for shrews exceed 557.

BADGER, *Taxidea taxus* Schreber. — "In early days," wrote Seton, 1929, "there was at least one badger for every square mile of high dry prairie in Manitoba and perhaps one-third as many on the heavy clay prairies on the Red River valley." The highest of these two figures gives a per-acre factor of twelve which is about one-fourth that of minks and longtailed weasels. Whether the above density of badgers is an economic one depends on the time element which Seton did not state. It may be a one-year economic density, that is, a badger may commonly require one full square mile during the course of a full year.

RED FOX, *Vulpes fulva* (Desmarest). — Grinnell, Dixon and Linsdale, 1937, quoted an experienced trapper who stated that after trapping for many

seasons on the best of the red fox country in California, he believed that on the average there was about one fox to each square mile and that under favorable circumstances three or even four foxes may be trapped in a single square mile. Whether the latter figures represent the population there or just the number of foxes that can be trapped on such an area over a period of time is not made clear.

One fox per square mile implies a per-acre factor of 5 or 6, and four gives a factor as high as 25.

Seton, 1929, estimated populations of red foxes at one per square mile without stating time of year, but he was apparently thinking of breeding pairs near or during the breeding season. Yeager, 1937, guessed the number at nearly two and a half per square mile, evidently soon after young foxes were independent.

Errington, 1933, estimated one red fox to 2.5 square miles of farming country in Iowa.

Scott and Selko, 1939, were the first investigators to make a serious and extensive attempt to actually census this species. Using approximately the same method as for skunks, they counted all dens containing litters which experience indicated averaged four young each. They found six red fox dens on the 65 square miles inspected, and calculated two parents and one unproductive adult for each den along with the four young, or 42 foxes in all. This represents one animal to 1.5 square miles and yields a per-acre factor of 40.

ARCTIC FOX, *Alopex lagopus* (Linnaeus). — Bertram and Lack, 1938, estimated the population of Arctic foxes between June 20 and August 10 as "about 12" on Bear Island which is about twenty-four square miles in area. Their figure is a subeconomic density figure since not all of it is accessible for use to the foxes, some of the area being lake or crags. The factor is about 30.

GRAY FOX, *Urocyon cinereoargenteus* (Schreber). — Errington, 1933, found an unusual winter concentration of gray foxes by tracking them during winter and early spring when snow lay on the ground, there being twenty-seven grays on five square miles, or between five and six to one square mile. This gives a per acre factor as high as 40, provided the gray foxes were using only the acreage recorded. Some may have been using additional surrounding territory.

COYOTE, *Canis latrans* Say.—Seton, 1929, wrote that "each pair of coyotes has a home range of 20 or 30 square miles" and that "probably the home ranges of at least half a dozen pairs overlap which assumes a general population of ten pairs to the township." Weighing about thirty-five pounds, they give a per-acre factor of about 35, possibly economic since they may cover such territory thoroughly.

Edge, 1935, estimated one per thousand acres, and the factor derived from his estimate is 60.

Comegys, 1904, quoted by Seton, 1929, described a coyote drive in which 40 coyotes were rounded up on twenty square miles in eastern Colorado, yielding a per-acre factor of 85. This is the highest so far derived for relatively pure predators.

BOBCAT, *Lynx rufus* (Schreber).—Seton, 1929, states that the home range of a bobcat is more than one thousand acres where food is plentiful, giving a home range factor of 10 and indicating that the per-acre economic factor for bobcats cannot be much less than 10, since home ranges overlap greatly.

SUMMARY OF PRIMARILY INSECTIVOROUS AND CARNIVOROUS SPECIES

Mole populations, as measured to date, commonly yield per-acre factors of from 50 to 1225. No home range or home territory data are available to rough out the picture of actual use of the areas on which they occurred. Some of the highest figures may be the result of drift into the census areas while censusing was progressing.

Shrew populations as measured to date commonly yield factors of from 45 to 880 with indications that factors higher than 200 are due to drift. Burt and Blair found that home ranges of mole shrews averaged 0.4 acres in Michigan, which indicates that per-acre economic factors are generally above 55. Home territories were not measured to indicate to what extent overlap of ranges occurs, hence what low economic densities may be.

Skunk population studies indicate common factors of from 130 to 285. Indications are that the home range factor is in excess of 140 and that therefore factors above this may generally be economic. The highest factors were evidently measured with greater accuracy than the highest factors for moles and shrews, having been more under actual observational control.

In general, it may be said that most of these insectivorous species maintain moderately high population and therefore, moderately high per-acre factors.

Per-acre factors derived from population data on those predatory species which are not chiefly dependent upon insects as food vary from a low of 8 to a high of 85, the latter being for a population of coyotes.

Errington found populations of gray foxes totalling five or six to the square mile, yielding a factor of about 40.

Little home range or home territory data is available to provide home range or home territory factors.

Available data indicate that densities of the carnivorous species are at least as low and possibly only one-half as much as those of the more insectivorous types. They lie below 100 whereas those of insectivores may rise to 200 and omnivores to 1000. It must be added, however, that although shrews and moles have been much studied, these studies were not generally so framed as to be conclusive.

Phytophagous Species

WOODCHUCK, *Marmota monax* (Linnaeus). — Seton, 1929, estimated a common woodchuck population at one to five acres. Burroughs and his neighbors, according to Seton, "accounted for" about 200 on a hundred acre tract during a single summer, which to Seton meant about 3 per acre. Hamilton, 1934, estimated five per acre. Coupled with an average weight of 6.5 pounds, these give factors of 590, 8850, and 14755. The latter are the highest factors so far studied.

Twitchell, 1939, found a greatest density of one woodchuck to about eleven or twelve acres, adding that he found no concentration which even remotely approximated the density found by Hamilton. Most of his densities were even less than one to twelve acres.

Home range sizes throw some light on these numbers. Woodchucks do not often travel more than 100 yards from their central dens and very rarely more than 200 yards. Generally, therefore, the home range amounts to only six to twelve acres which is about the highest rate of occupancy quoted by Twitchell. When a woodchuck travels farther, his home range is generally not 400 yards in diameter, but rather long and narrow. There is some likelihood that the home range is not greater than six acres. Twitchell had censused in country much of which was actually uninhabited by woodchucks and his populations are therefore subeconomic.

ROCKCHUCK, *Marmota flaviventris* (Audubon & Bachman). — Seton, 1929, found "at least 100 rockchucks on a two hundred yard rock pile in Yellowstone National Park," attesting to the numbers which this herbivorous species can attain. He did not record how much additional territory these individuals took in in their feeding, but since these animals do not go far afield in their grazing, it is probable that it was very little. A very high factor is suggested.

GOLDEN-MANTLED GROUND SQUIRREL, *Citellus lateralis* (Say). — Gordon, 1938, live-trapped, marked, and released golden mantled ground squirrels for further count and observation in Oregon. At one study area he subsequently found 17 marked and at least two unmarked squirrels occupying an area of about four acres. The rate of occupation was therefore about four to the acre, and the factor for these 187 gm. individuals, is 748.

On another sandy area in Colorado he found 10 marked and at least 15 unmarked squirrels on a ten acre area, or a rate of 2.5 squirrels per acre yielding a factor of 468. Being down in the hundreds, these factors are considerably less than those of the woodchuck whose factors run into thousands. This ground squirrel appears to be less herbivorous than the woodchuck.

BEECHY GROUND SQUIRREL, *Citellus beecheyi* (Richman). — Horn, 1938, stated of the Beechey ground squirrel that "on some hillsides from 5 to 10 per acre could be found" and the "along canyon sides, especially near

water, it was not uncommon to count from 20 to 25 per acre." He added that studies conducted by the U.S. Biological Survey showed that six ground squirrels per acre take 48 per cent of the forage annually. This was apparently a common population rate.

These squirrels weigh about 635 grams giving per acre factors of from 3175 to 6350. Running in the thousands, these figures are similar to those of woodchucks. These squirrels appear to be more similar to woodchucks in food habits than to the more omnivorous and spermivorous golden-mantle.

COLUMBIAN GROUND SQUIRREL, *Citellus columbianus* (Ord). — Shaw, 1920, stated that, where and when uncontrolled, Columbia ground squirrels may number as high as 25 per acre. Averaging about 454 gms., such a population yields a factor of 11,350. Like woodchucks and Beechey ground squirrels, their factors run into thousands.

RICHARDSON'S GROUND SQUIRREL, *Citellus richardsonii* (Sabine). — Seton, 1929, concluded from a count of 50 burrows in an area of 10 yards by 20 yards that adult Richardson's ground squirrels occupied a colony at a rate of 600 to the acre. How long was not noted, but the area thus occupied was extensive and apparently an economic density. Such a population of these ground squirrels which weigh about 340 grams when not fat, would yield a per-acre factor of 204,000, a remarkably large figure. This is the highest factor so far recorded for herbivorous species, running into hundreds of thousands. It is probably not a long-enduring population.

It is possible that two burrows do not represent one of these ground squirrels and that the true factor is therefore actually lower.

Seton estimated that in various other places, these ground squirrels maintained populations of 10, 25, 30, and 50 per acre. Their average weight being about 340 g., factors for such populations are about 3400, 8500, 9200, and 17,000.

TOWNSEND GROUND SQUIRREL, *Citellus Townsendii* (Bachman) — Couch, 1928, found Townsend ground squirrels exceedingly numerous near Lacrosse, Washington, during the spring of 1927, and, after treating a ten-acre tract with poisoned grain found 1,132 of these ground squirrels dead two and one-half hours later. Three days later he found 574 more dead on the same field without recording whether they were individuals which had drifted there from the outside. Nevertheless it appears that the population per acre was about 113, which somewhat exceeds that estimated by Kennicott for the thirteen striped ground squirrels.

Because Townsend ground squirrels appear to average about 255 gms., possibly more, the factor for them is roughly 2285. Like other primarily herbivorous species, the known factor for this species runs into thousands.

OREGON GROUND SQUIRREL, *Citellus beldingi oregonus* (Merriam). — Grinnel, 1919, estimated that Oregon ground squirrels attain populations of

about 110 per acre. Weighing about 454 g., such a population yields a factor of 49,895. This is one of the highest factors so far discussed, exceeded only by factors derived from Seton's estimate of Richardson's ground squirrel numbers.

SAY'S ROCK SQUIRREL, *Citellus variegatus grammurus* (Say).—Cahalane, 1941, used the trap removal census method similar to that used by Bole but with a line of guard traps surrounding it. His thought was that the line of guard traps "would attract and catch such small mammals as lived outside that might attempt to go within the boundaries" of his census area. He reasoned that the number of plot residents moving out of the census area and getting caught in the guard traps would be small since most of them would be taken in traps actually set on the census area. His purpose was to get a general picture of the mammalian composition of various type areas with the idea of finally estimating the entire population of small mammals over extremely large areas. In many cases these figures would run into such large numbers that a few thousand individuals more or less of one kind or another meant little.

His samples plots averaged relatively large as compared with those used by Bole for a similar undertaking and may accordingly have been more accurate, but because the supply of traps was insufficient to cover the entire plot at once, removal of the animals was accomplished by stages. The line of guard traps, also insufficient to be thrown at once around the entire plot was moved along down the sides as the trapping on the plot progressed. The guard strip was three meters distant from the outer boundaries of the census plot and was supposed to attract any animal passing by within about 1.5 meters on either side. Cahalane estimated a density of these animals at 1.6 per acre. The purpose and nature of his study indicate that this is a subeconomic density, at least for so short a period as the duration of his census.

THIRTEEN-STRIPED GROUND SQUIRREL, *Citellus tredecimlineatus* (Mitchill). — Kennicott, 1855, ventured the guess that striped ground squirrels numbered from 50 to 100 per acre, probably having in mind the numbers immediately following appearance above ground of young of the year. Such numbers, coupled with the average weight of 193 grams per squirrel, yield per-acre factors of 9,650 and more. The likelihood is that 100 per acre is neither a common nor long-sustained population. As for other primarily herbivorous species, this factor lies in the thousands.

Wooster, 1939, making a survey of the mammalian composition of a prairie in Kansas, estimated 1952 per square mile or 3.5 per acre. Weighing about 100 grams apiece according to Wooster, they yield a per-acre factor of 350.

The fact that Wooster censused sample areas in an extensive prairie indicates that much of it might have been unoccupied by this ground squirrel and that the 350 factor is somewhat below a true economic figure.

BLACK-TAILED PRAIRIE DOG, *Cynomys ludovicianus* (Ord). — Merriam,

1901, estimated numbers of prairie dogs of the great plains as averaging 25 per acre within areas covered by their colonies. Weighing about 1135 grams, they yield per-acre factors of 28,375.

ZUNI PRAIRIE DOG, *Cynomys gunnisoni zuniensis* Hollister.—Taylor and Loftfield, 1924, state that careful counts of Zuni prairie dogs indicated that an infestation was around 25 individuals per acre. They weigh approximately 759 gm., giving a factor of 18,975.

WESTERN CHIPMUNK, *Eutamias dorsalis* (Baird). — Cahalane, 1941, concluded from his trapping of 0.6 acre of yellow pine community that it was occupied at the rate of 0.8 to 8 western chipmunks per acre. The first figure is probably not an economic density figure but the latter may be because it was derived from an extremely small area which was uniformly good for chipmunks. It is almost axiomatic that if a particular method or area yields economic density data for one species, it will not yield economic data for most other species. Cahalane therefore obtained subeconomic data for most of the several species studied.

LEAST CHIPMUNK, *Eutamias minimus* (Bachman).—Seton, 1929, writing of this very small species, found a pair living in a little isolated thicket "about 20 yards in diameter." At Carberry, Manitoba, he estimated that an acre-large clearing surrounding an old sawmill held not less than 1,000 of these little animals.

EASTERN CHIPMUNK, *Tamias striatus* (Linnaeus).—Seton, 1929, drawing on his wide experience, estimated the numbers of Eastern chipmunks as varying from 2 to 14 per acre in more or less natural areas and from 20 to 30 in protected areas around his cabin. These yield factors of 170, 1190, 1700, and 2550. Bole, 1939, using killing traps for three days on half acre squares of land, estimated populations as high as 8.7 per acre in upland forests following a year of great seed production by the trees. Other estimates by him are 1.4 per acre and 0.8 per acre. His lowest estimate, 0.8 per acre for this species whose individuals weigh about 85 grams, yields a factor of 68, and his highest estimate yields a factor of 740. Seton's highest estimate of 14 per acre on areas away from human habitations yields a factor of 1190.

Burt, 1940, fearing drift due to withdrawal of chipmunks from the census area, live trapped them, made his records and released them to guard their territories against invaders and to furnish more information on the extent of individual territories. Having gotten his data incidental to similar investigations on the woodland deer mouse, he was able to indicate the home range size of only six individuals, not, admittedly a large number but accurately measured for that number and sufficient to fix the approximate size. The average diameter of the home range of the six was 93 yards, and the area enclosed was 1.2 acres. This allows a theoretical lower economic limit of 0.8 chipmunks per acre, the lowest found by Bole, and also by Burt by his live censusing method.

Of his findings Burt wrote, "My data on populations of chipmunks do not cover an area sufficiently large to represent conditions accurately. They do, however, give a rough indication of the population per acre and for that reason are presented here." They are the best rounded data the writer has at hand, and they may be used within their limitations. The two areas studied by Burt were isolated woodlots, and the areas were therefore defined and the counts of chipmunks complete. Results from the two areas were added together. The combined population varied from 0.8 per acre in the spring to 3.6 during the early breeding season. The average yearly population was two per acre, giving a low factor of about 70, an average factor of 170, and a high factor of 310. Burt suspected, though he did not census the areas after August, that the population might become somewhat higher during the second bearing period in late summer. No home territory data are available to show the possible lower limit of economic factors, but factors derived from Burt's data are notably low.

RED SQUIRREL OR CHICKAREE, *Tamiasciurus hudsonicus* (Erxleben). — Klugh, 1927, stated that in the original pine forests and maple beechwoods of Ontario he would place the abundance of the red squirrel at not more than one to every twenty acres. In the spruce woods of New Brunswick there were as nearly as he could ascertain about two to every hundred yards square. At Grand Bent, Ontario, in a piece of mixed forest of hardwood and softwood trees he found more of this species than he had seen at any other place, a census showing nine per acre in the spring. This species averages about 254 grams, and the per-acre factor for the population is 2,290.

Dice and Sherman, 1922, also reported the numbers in various types of cover, the numbers of squirrels varying from one per acre in black ash swamps, hemlock forests, white pine forests, scrub stage of hardwood forests; two per acre in black spruce-tamarack bogs; three per acre in cedar swamps and birch-aspen woods; seven per acre in dry hardwood forests; and nine per acre in wet hardwood forests. Factors vary from 255 through 510; 760; 1,780; and up to 2,290.

Hornaday, 1913, recorded about one to four acres after the population had been reduced by an extermination campaign.

Hatt, 1929, estimated two to nine acres; two to six acres of mature, dense, white pine stand; one per acre of spruce swamp; one to each acre-and-a-half of hemlock, and one to each two acres of mixed forest.

Baumgartner, 1938, found 34 to each 100 acres of unpastured woodlot or about one to three acres.

Bole, 1939, using half-acre quadrats and death traps for three day periods, estimated 1.7 red squirrels per acre.

Most of these estimates and censuses quoted for the red squirrel were of the sampling type, designed to show mammalian composition of the various cover types named. Some of them accordingly included large areas which were not habitats of these squirrels. Many included areas that at some time

or other, or even at the moment of the census, were suitable habitat but were not inhabited by the squirrels. A few, notably the highest concentrations quoted, turned out to be censuses or estimates of numbers on habitats in use, hence are of economic densities. This happened, not entirely accidentally, but because those censuses which are not aimed at discovering the mammalian composition of a cover type, are aimed at discovering economic densities and thus tend to eliminate some of the more obvious kinds of unused areas in a squirrel's range.

Where the lower limits of economic density occur cannot of course be defined by methods commonly used for determining either of the above kinds of populations.

Two hundred and 50 yards or about 13 acres square is said by Klugh to be the usual home range.

Seton estimated "less than 10 acres" and stated that many red squirrels pass their whole life in an orchard of four or five acres. Hamilton, 1939, stated that "in areas where sufficient food is found an acre of territory will suffice." He found six living in a three-acre oak and maple woodlot near Ithaca, from which young moved as they matured. On the Cornell University campus he found two, three and sometimes four occupying a clump of maples, all spending the greater share of their time within the bound of an acre. One group of oaks only half an acre in area there supported eight of these squirrels which seldom travelled more than a few rods from the trees.

It is evident that although many home range studies of one sort or another have been made, there is little agreement between them. Some of this is due to very casual observation and some, of course, to observations under widely different conditions and of varying lengths of time.

As Hamilton states, organized marking and observation of more individuals in a wide diversity of habitats can add much desirable and important information. Indications are that the average monthly home range of an individual is small, perhaps usually less than four acres, and that overlap is considerable.

GRAY SQUIRREL, *Sciurus carolinensis*, Gmelin. — Gray squirrels, slightly larger than chickarees and generally inhabitants of dense shrubby lowland woods, maintain populations of about three to the acre in Central Park, New York City, according to Seton, 1920. Such a situation is highly artificial; the squirrels are undoubtedly maintained at a high level by artificial feeding.

Goodrum, 1937, stated that the density of squirrels, probably grays although he made no statement to that effect, in a protected river bottom area was two per acre. In open river bottoms the density was 0.8 per acre and in open upland 0.5. In determining these figures, his chief method was to observe a known area for 30 minutes at a time when squirrels were most active. In 1940, he reported estimating populations of this squirrel by time area counts used for his earlier reports; they yielded estimates of 1.4 squirrels per acre of hammock; 0.9 squirrels per acre of poorly drained bottom, and 0.7 squirrels per acre of well drained bottom.

Chapman, 1938, wrote, "The summer squirrel population on a 41,000 acre area, calculated from data on sample plot or spot counts and leaf nests, was 0.7 squirrels per acre; 0.2 per acre; 0.3 per acre during different years.

Adults, according to him, weigh about 500 grams, indicating that per acre factors may vary from 350 to 1000. Chapman's figures indicate lower factors but neither writer indicates conclusively where the lowest economic density lies. Goodrum's lowest population concentration, 0.2 per acre, yields a factor of about 100.

FOX SQUIRREL, *Sciurus niger* Linnaeus. — Goodrum, 1937, reporting on more or less combined population of gray and fox squirrels without stating the exact ratios of the species, stated that they varied from 2 per acre in protected river bottom to 0.5 per acre in open upland creek areas. It is probable, however, that the fox squirrels were not inhabiting the protected river bottoms nor grays the upland creek areas. Intermediate habitats were inhabited by both. One fox squirrel to two acres gives an economic factor of about 400.

Baumgartner, 1938, found 0.7 and 0.8 to the acre of woodland in Ohio. The average weight of adults being 814 gms. according to him, factors of 560 and 650 are apparent for these populations, which lie between those established for grays.

Seton, 1929, quotes a warden as estimating 500 fox squirrels to 100 acres, or 5 per acre. It would be interesting to know how long an acre will carry such a concentration. The factor of 4070 is probably an artificial or short-time one, not due to natural conditions.

Allen, 1938, found two to the acre of open oak woods in Michigan.

Bennett and Nagel estimated one squirrel per two acres of woodland and one per eight acres.

Allen's figures allow a factor of about 1628 and Bennett and Nagle's allow about 100 to 410.

Home range information for neither squirrel is sufficiently organized to indicate just what subeconomic densities may be, but it is notable that these men, all working in habitat which is more or less uniform for squirrels and more or less obviously squirrel habitat, found no population so low as to give a factor less than 100. High factors run in the lower thousands but not consistently as high as factors for herbivorous ground squirrels.

SOUTHERN FLYING SQUIRREL, *Glaucomys volans* (Linn.).—Seton, 1929, wrote that in his Connecticut woods he has found more than once three flying squirrel nests within a radius of 50 yards and concluded that there were three families within one acre.

A complete annual family consists of five or six individuals in all immediately after the first young are born. The entire lot, with an adult weight of about 55 gms., would give per acre factors of 275 to 330.

Burt, 1940, using a live trap-marking-retrap method similar to that he used

for mole shrews, found one adult female, two young females, and three adult males or a total of six animals on a wooded plot of 3.72 acres during one summer. Each, excepting one which died, was caught three times from June 29 to August 14, indicating a 6 weeks population of from 1.3 to 1.6 individuals per acre. The areas in which he trapped were too small for him to establish definitely the home range of this species, and his data was so limited that he did not draw maps to show the extent of their use of the area. He remarked, however, that individuals of both sexes ranged over the entire 3.72 acres, indicating that it was in use. The lowest economic factor established for this species in this area varied from 75 to 90.

Bole, 1939, making a random census intended to be comparative from time to time and habitat to habitat, used killer traps for three-day periods on half-acre census plots. Southern flying squirrels, he concluded, at times averaged three per acre; 0.4 per acre; and as many as 6 per acre in "woodland habitats." His tables show four per acre most common. It is quite probable that his low number 0.4 per acre may be a subeconomic density, but his other figures fall within the top and bottom densities already discussed for this species. His most frequent figure, 4 per acre, gives a factor of 220. The fact that he did not name dates in discussing his census periods makes further comparison with the above data both uncertain and difficult.

SUMMARY OF PRIMARILY SPERMIVOROUS SPECIES

Spermivorous species frequently take large amounts of buds, some leaves, and considerable numbers of insects. Many supplement their seed diet with such great quantities of other food as to be omnivorous or nearly so. Apparently to the degree with which they are able to do this at times, they may maintain populations which yield factors into the low thousands. Under very favorable and long-continued seed producing conditions, they may reach and maintain the thousands. Generally, however, their factors lie in the hundreds.

Phytophagous Species (Continued)

WESTERN POCKET GOPHER, *Thomomys bottae* (Eyedoux & Gervais). — Cahalane, 1941, estimated populations of this pocket gopher at 0.3 per acre. The purpose of his study, the method of censusing, and our knowledge of the manner of utilizing territory show that this was not an economic density.

NORTHERN POCKET GOPHER, *Thomomys talpoides* (Richman). — Seton, 1929, estimated northern pocket gopher populations at from 2 to 3 per acre in one area studied and from 5 to 10 per acre in another area. Average individuals of the species weigh approximately 140 gms. and factors based on this are as follows: 280, 420, 700. Being in the hundreds, these are relatively low for primarily herbivorous species.

UPPER MISSISSIPPI POCKET GOPHER, *Geomys bursarius* (Shaw). — Bailey, 1895, stated that where he had estimated numbers of upper Mississippi pocket gophers there were three or four to the acre.

Butcher, 1921, estimated that good clover or alfalfa fields might have an average infestation of from 10 or 15 per acre in Iowa.

Mohr and Mohr, 1936, trapped pocket gophers from a poor three-acre field of alfalfa until no more new mounds were being thrown out by these creatures. This field, isolated by the width of about 300 yards from any other gopher bearing area, yielded 13 individuals, a rate of about four per acre. On another 1.46 acre area of more or less natural prairie along a railroad right of way he caught eight gophers which had thrown out 303 mounds. Having counted 1652 mounds on ten acres of surrounding prairie, he concluded that the entire prairie bore gophers at a rate of between four and five per acre during early October while the young were still numerous. This perhaps accounts for a higher level than that claimed by Bailey who was evidently thinking of breeding pairs.

During October the adults averaged about 350 gms. the populations of three, four, and five gophers yield per-acre factors of 1050, 1400, and 1750. Applied to Butcher's figures for areas which were probably 100 percent gopher forage acreage, they give a factor as high as 5250.

Without stating by what means he arrived at such figures, Gunderson, 1941, wrote of average infestations of 10 to 15 gophers per acre in Iowa. He was probably quoting Butcher, 1921. Running in the thousands, these factors are characteristic of herbivorous species.

BANNER-TAILED KANGAROO RAT, *Dipodomys spectabilis* Merriam. — Monson and Kessler, 1940, made den counts and excavations of 70 dens of the banner-tailed kangaroo rat in southeastern Arizona and southwestern New Mexico during the period from March, 1935, to August, 1936. Although each banner-tail den gave every indication of being in use, actually only 44 contained bannertails. The authors explained that this might be because the bannertails were not at home at the time or because they were overlooked while the excavating was being done. Usually only one bannertail was found in each of the occupied dens. Three dens, however, contained two apiece, all adults.

The tone of the article implies that all individuals found in this study were adults, and the findings yield a factor of one bannertail to 1.5 dens. "Densities of one den per acre are confined principally to small areas," according to them. One den per acre points to a population rate of 0.7 bannertails per acre which, weighing about 115 grams, gives a factor, apparently economic, of 80, since they wrote of densities of one den per acre being confined principally to small areas.

Vorhies and Taylor, 1922, had previously estimated population of this species at 2.4 per acre by counting the number of dens over many acres which looked like good habitat and by assuming that each den which they counted was occupied by one individual. They were presumably thinking of adults or breeding individuals when making their counts. Taylor, 1930, later set the number lower at 2 per acre. Since his census was made to sample extensive land areas, it is probable that it was not economic, yet one is left at a loss

to reconcile these findings with those of Monson and Kessler. If this figure of one kangaroo rat to 1.5 dens is applied to the findings of Vohries and Taylor, the compromise population is 1.6 rats per acre, giving a factor of 230. If, on the other hand, the Vohries-Taylor estimate of one rat per den is correct, the Monson and Kessler factor is low and should be 115. The difference is not, however, great in view of the fact that small rodents may easily double their economic density for long periods. One may then take special note of 80 as being a possible low economic factor.

Cahalane, 1941, estimated populations of this kangaroo rat at 1.5 per acre. The factor is 170. The species is primarily spermivorously, and its factors run in the hundreds.

MERRIAM'S KANGAROO RAT, *Dipodomys merriami* Mearns.—Monson and Kessler, 1940, also attempted a census of Merriam's kangaroo rat by making counts and excavations of dens in southeastern Arizona and southwestern New Mexico between March, 1935, and August, 1936. Dens per acre ranged from 8 to 53 with an average of 31.3 on the thirty-three one-acre plots in various localities where the kangaroo rats were considered common to abundant. Of 74 den excavations, only 18, or about one-fourth, yielded this species, and in no case was more than one rat found in an occupied den. The authors felt that they might have overlooked some of the animals when excavating and might also have misidentified some of the dens but figured an average of one inhabitant per 4.11. They failed to state if the individuals counted were adults or nestlings but the general tone of the article implies adults only. Their factor of one kangaroo rat per 4.11 dens indicates that populations in the plots examined, ranged from almost two to almost twelve in areas where this species was common to abundant. Because they were interested in a subeconomic density study of a given type of country, their lowest density figures may not have been economic, hence the lowest factor of 90 is difficult to evaluate. We may note, however, that it practically is the same as the lowest economic density factor which is derived from their bannertail census. Their highest density figure for the small species is 540, considerably higher than that for the bannertail.

CANADA PORCUPINE, *Erethizon dorsatum* (Linnaeus).—Struthers, 1928, found twelve colonies of Canada porcupines, "each of not less than 50 individuals" along with many isolated family groups of half a dozen or so in a region abounding with hemlock forests and deserted farms all within a radius of two miles. This calculates out to more than 50 per square mile. Adults weighing about 16.7 lbs., according to Seton, 1929, the per-acre factor would be in excess of 510.

Cox, 1923, quoted by Seton, stated that foresters in Minnesota were able to make a fairly accurate count of porcupines during winter. On 26 forty-acre management areas they found 76 porcupines or an average of three to each forty acres. The per-acre factor was in excess of 640.

These are notably low for an herbivorous species, and more home range data may indicate that economic factors are much higher.

YELLOW-HAIRED PORCUPINE, *Erethizon epixanthum* Brandt. — Taylor, 1935, found that yellow haired porcupines may be present in an area in some numbers at one time of the year but entirely absent there at another. Records of exceptional numbers, he found, are usually for limited areas, naming as examples 22 killed in a single quarter section and 23 killed on 15,000 acres, implying by this that all were killed within a sufficiently short time so that they might have been occupying the areas, not migrating into it from elsewhere. If so, the numbers measured from one per seven acres downward. There may have been others unkilld, indicating greater numbers than one per seven acres.

Taylor found more frequent populations around 3, 8, and 15 per section or as many as one to forty acres. The per-acre factors vary from near zero to about 190. Many of these populations were apparently subeconomic.

PRAIRIE DEERMOUSE, *Peromyscus maniculatus* (Wagner). — Blair's 1940 maps show that populations of the prairie deermice reached a three-weeks minimum density of 18 mice on a nine acre census plot in September but, occupying only 5.16 acres of the area, their economic density was as high as 5.3 per acre. Adult mice of this species weighing about 16 grams per-acre three-week economic factor of 85 are indicated. Certain short-cuts used by Blair in outlining the home ranges of the mice on maps make the home ranges appear larger than it may actually have been if measured in a more restricted method. The average home range being little in excess of half an acre, and the amount of overlap being great, indicates that 5.3 mice per acre is about as low as economic densities of this species are likely to get. That it frequently gets considerably higher is indicated by a one-month economic density of 12 mice on 0.77 acre in July, or a rate of about 16 mice per acre with an economic factor of 155. During the following month Blair found only 9 adult mice occupying the entire area, giving a one-month economic density of 12 mice per acre and a one-month economic factor of 192.

Townsend, 1935; Bole, 1935; Wooster, 1939; and Dice, 1939, censused populations of various other varieties of the prairie deermouse. Wooster did not detail his methods of censusing except to remark that he used ordinary mouse traps on quadrats of 200,000 square feet at all times of the year and on all kinds of prairie habitats for 30 days at a time on each quadrat. He included blanks in his calculations of density, hence his estimates of 1728 deermice to the square mile or 2.7 per acre is a subeconomic density figure, the factor is about 45. Dice and Townsend, undoubtedly included larger blanks because they wished to estimate the total population on varied habitats, hence also obtained subeconomic density figures.

Bole also included blanks of varying and unrevealed size but some of his figures are so recorded as to be subject to conversion. His highest figure obtained in the same manner as for shrews is 22 per acre with a factor of 350, but this may be subject to a slight downward revision to 16 per acre according to Dice's formula. His figure of 4 per acre is slightly higher than Blair's economic density figure of 3.2 per acre, but certain others which he mentions

are lower than the home range density, hence are obviously based on sizeable blanks. This species is quite omnivorous, taking large quantities of insects along with considerable seeds and nuts and some green food. The more reliable censuses indicate factors in the low hundreds similar to those of squirrels.

Peromyscus maniculatus rufinus (Merriam) and *Peromyscus boylii rowleyi* Allen.—Cahalane, 1941, estimated mixed populations of these species at 14.6 per acre, basing his estimate on methods described for his study of the Western chipmunk. At another point he estimated *P. boylii rowleyi* alone at 3.9 per acre.

WOODLAND DEERMOUSE, *Peromyscus leucopus* (Rafinesque). — One of the most careful studies of populations of seedeating species is that by Burt, 1940, on the woodland deer mouse. Burt marked the animals, recorded the spot at which they were caught, and released them there to get further records on the extent of their home ranges. His published maps show not only how many mice were on the census area but also how much of the area was actually in use as well as the length of time of the census. This information permits calculation of both ceiling and floor of economic densities at definite periods of the annual cycle of numbers.

The home-range maps show that a population of 13 of these deer mice occupied practically all of an area of 1.8 acres between August 11 and October 15 but that smaller populations were inclined not to use all of the area even though it appeared to be a least at times all good habitat for the species. The lowest rate at which a population used the entire area was during the period from July 7 to July 27 when there were only eight mice on the area, occupying only 1.6 acres of it, making the lowest economic density recorded for this species, 5 per acre. The weight of the adult mice being approximately 22 grams, the lowest economic factor was 110.

The highest economic density was one of 7.4 mice per acre when a month-long census showed that 11 mice were occupying only 1.4 acres of the area. The economic factor for this high figure is 165.

Another census of 1.5 months duration beginning August 11 showed that the increased number of mice, due to the full breeding season build-up, spread throughout the area, occupying it at the rate of 7.2 mice per acre with a factor of 160.

Because of the completeness of Burt's study it is of interest and value to compare his density figures with his home range and home territory figures.

The home range, as defined by him is that area about its established home which is traversed by the animal in its normal activities of foraging, mating, and caring for its young. It excludes those areas merely traversed while in search of home sites or for other temporary causes.

The home territory is that area protected by these mice against invasion by other adults of the species. For this species home range and home territory were equal in area.

Burt found that the average monthly home range of 65 adult females was 1012 square yards and of 58 adult males, 1412 square yards. The average between these two figures is 1162, or 0.24 acre. The home ranges of the mice did not overlap, and the lowest economic concentration theoretically possible is four mice per acre. As for prairie deer mice, factors lie in the low hundreds.

COTTON RAT, *Sigmodon hispidus* Say & Ord. — According to Stoddard, cotton rats may, in such favorable habitats as heavy broomsedge stands, reach a concentration of around 40 per acre. Weighing about 170 gms., they give a per acre factor of 6720. As for other herbivorous species, factors lie in the thousands.

WHITE THROATED WOODRAT, *Neotoma albigula* Hart. — Monson and Kessler, 1940, found 2.57 dens of the white-throated woodrat per acre on a 750 acre tract in southeastern Arizona and southwestern New Mexico sometime between March 1935, and August, 1936.

Eighty-two of the dens were examined over a twelve-month period, but most of them were examined in July and August. Only 56 were occupied. As time passed, they found 167 or 91.4 per cent occupied, each usually containing only a single individual, presumably more or less adult, but females with young were found in four instances. Implication was that 91.4 per cent of the dens contained 1 adult rat apiece, and the population average of the whole area was about 2.4 white-throats per acre, giving a factor of about 480, since the rats weigh about 197 grams. White throated woodrats are primarily herbivorous. The low factors may be due to the fact that the study was not of an economic density or to sparsity of vegetation, probably the former. Cahalane, 1941, estimated white-throated woodrat populations at from 1.2 to 2.3 per acre. The factors are about 240 and 460.

Spencer and Spencer, 1941, found that dens of white-throated woodrats in Arizona varied from none up to twenty per acre and evidently calculated a rat per den when writing of a peak population of 20 rats per acre in the area. Weighing about 199 grams, peak populations would yield a per-acre factor of about 3980.

This is the one factor for this herbivorous species which lies in the thousands. No home range data on other land-use figures for this species appear to be available to show possible lower limits of economic densities and factors.

MEXICAN WOODRAT, *Neotoma mexicana* Baird. — Cahalane, 1941, estimated populations at 1.6 per acre, basing his estimate on methods used also for the western chipmunk. The purpose of his study and the method indicate that this figure definitely does not represent an economic density. Extensive blanks were included in his population density calculations.

LEMMING MOUSE, *Synaptomys cooperi* Baird. — Stegemen, 1930, concluded after trapping an area with snap-back maps that areas occupied by lemming mice bore populations of about 14 per acre. His map, not as detailed as those by Burt and Blair, did not show home ranges but did show how

spotty was the distribution of this species within an area of a few acres, all of which looked superficially very much as though it were lemming mouse habitat. These mice weigh about 22 grams, and a per-acre factor based on this population is about 310. The nature of the study, including a critical elimination of certain parts of the census area which seemed unoccupied, indicate that the density of 14 per acre was an economic one.

Bole, 1939, found four per acre, six per acre, and 1.5 per acre. Five and six per acre appear to be economic densities, but 1.5 definitely is not, although no home range and no censuses appear available to show where the limits between economic and subeconomic densities lie.

RED-BACKED MOUSE, *Clethrionomys gapperi* (Vigers). — Townsend, 1938, estimated from 9 to 58 red-backed mice per acre.

PENNSYLVANIA MEADOWMOUSE, *Microtus pennsylvanicus* (Ord). — According to Blair, 1940, who used the live-trapping, record and retrap method for determining home ranges of Pennsylvania meadow mice, the average size of the home range of a female during the period of three weeks (Blair stated one month but, because he trapped only twice, in alternate weeks, the entire time elapsing between the beginning and end of his trapping period was only three weeks) during July, August, and September, was about one-fifth to one-fourth of an acre. The average male home range varied from slightly less than one-third of an acre to a little less than one-half, being greatest in dry areas. The average home range of a mouse during a three-week period is, therefore, likely to be about one-third of an acre, and, theoretically, no economic density population of this species is likely to be less than three per acre. The mice weigh about 40 grams, and the home range factor is 120. This exceeds that of 110 for Burt's figure for pine mice by only 10 points, hence is not essentially different.

Most of recorded populations of this species are considerably in excess of this low figure, partly because the home ranges overlap, and partly because these meadow mice are so successful in occupying ground that they are a relatively fool-proof species to census, as compared with lemming mice, for instance, whose distribution is exceedingly spotty. A series of traps planted in habitats of the more numerous and widespread meadowmouse are more likely to fall within an area uniformly occupied.

Blair found the following resident populations per acre: 3.5, 11.9, 10.0, 8.5, 9.2, 9.2, 5.8, 0.2, 0.6, 0.8, 2.2, 1.2, 2.2, 2.6. Densities less than three per acre are probably noneconomic. His highest find, 11.9 per acre, gives a three-week per-acre factor of 476.

Hamilton, 1937, estimated Pennsylvania meadowmouse populations in New York at 35, 55, 60, 35, 75, 80, 60, 100, 155, 55, 40, and 50 per acre over a four year period on an eight acre field supporting a heavy mature stand of alfalfa, the whole area having ideal cover for meadow mice. On a six acre field where orchard grass and *Festuca* formed a dense mat of excellent cover throughout the year he found 15, 20, 12, 12, 25, 35, 30, 50, 60, 60, 40, 8, and

13 per acre. On a twenty-acre orchard of young apple trees with ground cover principally of alfalfa, red clover, quack grass and orchard grass he found 25, 60, 110, 90, 50, 120, 140, 100, 70, 225, 240, 150, 70, and 80 mice per acre. The largest population, 225 per acre, gives an economic factor of 9000 which occurred during the early winter of 1935-36, a peak year for meadow mice. None of his estimated populations come anywhere near the theoretical lowest economic density of 3 per acre in average mouse habitat, the lowest being 12 per acre.

Townsend, 1935, using a method already described, estimated from 12 to 67 per acre in New York.

Greffenius, 1939, wishing to find the abundance of Pennsylvania meadow-mice in a field of timothy and other grasses, laid 356 traps on a 2.03 acre plot until no more mice were caught. He did not describe his method, time, duration or results in detail but estimated the population as 40 to 45 per acre.

MONTANA MEADOWMOUSE, *Microtus montanus* (Peale). — Piper, 1909, estimate a temporary population of Montana meadow mouse at from 800 to 1200 per acre, but not at the center of the outbreak where the number was undoubtedly smaller. This population was, therefore, an aggregation, not an economic density. Later he found from 200 to 500 per acre. The mice, weighing about 50.4 g., give per acre factors of in excess of 10,080.

CALIFORNIA MEADOWMOUSE, *Microtus californicus* (Peale). — Hall, 1927, estimated between 300 and 400 California meadowmice per acre during a time when housemice existed on the areas in plague proportions. These mice were migrating along with the housemice and apparently also existed in limited plague proportions.

HAYDEN MEADOWMOUSE, *Microtus haydeni* (Baird). — Wooster, 1939, estimated the Hayden meadowmouse numbers in Kansas at 2,462 per square mile, averaging three per acre. His census was designed to discover the composition of a prairie, hence was not intended to discover economic densities of this mouse. Indications being that their home ranges are smaller than one-third of an acre, it seems likely that Wooster's figures do not represent an economic density.

PINE MOUSE, *Pitymys pinetorum* (Le Conte). — These herb-eating mice commonly attain numbers of 200 to 300 per acre in more or less natural surroundings although such populations appear to be relatively short-lived. Hamilton, 1938, estimated the population of pine mice in a New York orchard at between 200 and 300 per acre, and 1937, estimated the populations of Pennsylvania meadow mice up to 255 per acre. The usual numbers are, however, lower.

Bole, 1939, quoted pine mouse populations at 18 per acre; 6.4 per acre and down to 0.5 per acre. His tables show figures of 4, 6, and 8.

Burt, 1940, found the normal home range of this species as about one-fourth of an acre, indicating that it is unlikely that an economic density is

less than four or five per acre, this indicates that the home range factor for these 27.5 g. mice is somewhere above 110 or about that which he found for woodland deer mice but roughly double that found by Blair for prairie deer mice. Bole's figure of 0.5 mice is therefore probably a noneconomic concentration.

MUSKRAT, *Ondatra zibethica* (Linnaeus). — Johnson, 1925, stated that muskrats commonly reach an abundance of five or six breeding pairs per acre and that in certain protected marsh areas in New York, "an estimate of as many as ten breeding pairs to the acre is no exaggeration." By "breeding pairs" he seems to imply adult populations which maintain themselves over long periods. His estimates indicate per acre factors varying from 7900 to 15800, the lower figure being approximately the same as the factor derived from Stoddard's cotton rat populations.

Pancoast, 1937, states that the normal catch per acre each year in wild marshes in Maryland is 3.5 and in ponds is 6 muskrats. Because trappers generally leave sufficient breeding stock for the coming year, this indicates that the lowest per acre factor is in excess of 2765.

Errington, 1938, reported a catch of 8.5 muskrats per acre of privately owned marsh in Iowa and estimated the population there during the following year at close to five per acre, probably during the fall when the annual crop of young swelled the population.

Butler, 1940, estimated the carrying capacity of Canadian marsh at from 3 to 26 per acre.

Errington, 1940, stated, "It has been observed that late in April and early May, mated pairs may concentrate on a considerable scale in parts of Round Lake, Iowa, that would be almost vacant later in the summer; with general marsh populations less than one pair per two acres, temporary aggregations have reached densities of five pairs per acre locally." From work carried on at Round Lake and Cheever Lake, both in Iowa, he concluded that about one pair per 30 to 50 yards constituted the peak breeding densities which muskrats will tolerate there. When breeding densities exceeded two pairs per acre intra-specific friction was common.

It is apparent that populations most generally quoted for muskrats regularly yield factors considerably higher than those for many other mammals; the home range estimates on this mammal also indicate a high factor. Seton, 1929, stated that the home range of each individual muskrat is less than 200 yards across which implies that even when there is no overlap in territories of individuals, a factor based on the home range is about 110, hence relatively large. Generally the home range is considerably smaller than seven acres.

HOUSE MOUSE, *Mus musculus* Linnaeus.—One of the greatest concentrations of mammals which are primarily seed eating in nature is one of house mice recorded by Hall in Kern County, California, during 1927. These mice were coming from the dry bed of a former lake in the center of an area about 18 miles in diameter. Impressive numbers of the mice, moving outward from

the lake basin as early as November, 1936, were succeeded by a smaller wave which appeared in December. A third marked wave moved outward into the surrounding country on January 6, 1927, the wave diminishing in strength toward the middle of the month.

The cause of the large build-up of the mouse population was more or less artificial, the lake having been drained three years before, and barley and kafir corn which grew there provided a more than usual abundance of seed as well as cover. Then, in the fall of 1926, sheep were grazed on the area, removing the cover and what little food the mice had not eaten, thus crowding them out.

Hall found 2099 housemice to the acre over much of the area of the lake some months after the migrations began. It is probable that this number did not actually build up on the spot on which it was found but had in some part moved onto this spot, bolstering the large population already there. If so they represent an aggregation.

In other parts of the lake basin there were 968 per acre, these being possibly representative of the population which had grown up there. Even the lowest population, 242 per acre, appears to have been a temporary one. Its factor was about 2,295, a housemouse averaging about 13.6 g. according to Hall.

JUMPING MOUSE, *Zapus hudsonius* (Zimmerman). — Blair, 1940, used the live trapping, marking and release method of studying populations of the jumping mouse, which Burt used for woodland deermice. He wrote of 13, 16, and 29 individuals on 9 acres at various times during the summer but mentioned that about one acre was occupied by a pond, and further added that they did not occupy about 3.2 acres of relatively arid blue grass on a steep hillside. Adding that "thus one can calculate the population per acre on the 5.8 acres on which the mice did occur" he concluded that the populations per acre averaged 0.2 late in May but increased to 2.8 early in June. A maximum population of 5.0 jumping mice per acre of the occupied part of the plot was reached late in June. In early July it was 3.4 and in late July, rose to 4.3. In early August it has fallen slightly to 4.0 and in late August was only 2.2. In early September it dropped to 1.4 but in late September it had again increased to 216 per acre. Animals which were caught only once were considered non-resident on the area, hence not counted as part of its population.

Blair implies by the statement, "one can calculate the population per acre on the 5.8 acres on which the mice did occur," that all figures, including the 0.2 mice per acre were economic densities. This population gives a per acre factor of 2.8, the weight of this mouse being 14.5 gms., but the lowest possible factor one may obtain from the average home ranges of 0.89 to 0.92 acres per mouse is about 13. Since many mammals have a population density about twice that of one per home range, one may conclude that jumping mice do not ordinarily reach an economic density of much less than two to the acre or a factor much less than 26. Evidently the 5.8 acres was not all occupied although it appeared to be and quite probably was good jumping mouse habitat. We cannot be sure how much higher than 26, the lowest economic per

acre factor is for this species. The highest density discussed by Blair is 5 per acre, giving an upper factor of 73 which is considerably lower than 110 obtained from Burt's figures for the lowest economic density of woodland deer mice. It is however somewhat higher than the two-week, per acre factor of 51 derived from Blair's lowest economic density of prairie deer mice. No maps are available to disclose the extent and duration of their use of the area, and no time factor is given except that the trapping, marking and note taking occurred early or late in stated months.

Bole, 1939, found a high concentration of 18 and mentions 12 and 3.5 as other concentrations obtained by his method, described before. Because his census figures were based on three day trapping periods the factors may be termed a three day, per acre factors. They vary from 50 to 263.

WHITE-TAILED JACK RABBIT, *Lepus townsendii* Bachman. — Mohr and Mohr, 1936, made a strip count or cruising census of white-tailed jack rabbit populations in Blue Earth county, Minnesota, and concluded that their numbers varied from about ten to about 80 per square mile. This census, like so many others, was intended to discover approximate numbers of these jacks for comparison from year to year, but not to solve the fundamental question of absolute animal populations or areal use. Even the highest number of jacks recorded in this paper was not an economic density, the jacks on the area utilizing winter wheat fields, clover or alfalfa fields, and fence rows for their sustenance but not all of the plowed fields, farmyards, pastures, and other areas which the writer had used in calculating his figures on density of the jack rabbits counted.

Factors based upon the above censuses vary from 50 to 310, adult white-tailed jack rabbits weighing about seven and one-fourth pounds.

Seton's data on home territory shed some light on the approximate common division line between economic densities and noneconomic densities. Each of the white-tailed jacks which inhabited his park kept closely to its own region often of fifteen acres although 120 acres were available for movement. At one jack per fifteen acres the per-acre factor is about 215; and at one per 10 acres gives 330. Overlap of home territories would set economic factors higher than this. It thus appears that Mohr & Mohr did not observe an economic density, since their highest factor is only about 310.

The writer wonders if any good purpose is served by converting most data obtained by strip censuses or by ordinary use of death traps for three day or any other period into estimated population densities per acre even though it is true that the absolute size of an animal population per acre or some other given unit is such an intriguing question. It appears that strip censuses and death trapping as generally carried out, do not solve the question of absolute populations and in fact merely confuse it. Such would-be censuses might often better be given as counts derived per mile (or other length unit) or as three day block trapping or other method. These are at once comparative within set limits and are not less useful for not having been converted to populations per acre or other unit. If knowledge of actual population is desired, it may

be acquired by some more reliable and time-consuming method plainly adapted to that end.

ANTELOPE JACKRABBIT, *Lepus alleni* Mearns.—Vorhies and Taylor, 1933, estimated combined populations of antelope and California jack rabbits in southern Arizona by counting all jack rabbits and also all cows seen during the course of a census, then using the jack-cow ratio in connection with the known number of cattle on the range to estimate the total number of jack rabbits. Operating mostly at times of the year when visibility was best, these authors made more than 50 jack rabbit counts covering a lineal distance of 238 miles. They quoted several population figures based upon their supposed ability to see various distances to either side of their path but settled on the estimate of 7,500 jack rabbits on 50,000 acres as their best and truest estimate. Six thousand six hundred and sixty-six were antelope jacks. This averages one antelope jack to 7.5 acres. Weighing about 8 pounds each, these give a per acre factor of 750.

This cannot be said to be an economic density because the writers remarked that concentrations of rabbits were more numerous in the mesa portions than in the foothill portions of the range for which they failed to keep separate counts. The economic density and factor at the time were therefore higher than the above figures.

Some, though confessedly not much, light is shed on this phase by the observations recorded by these writers. An observer followed one of these jack rabbits for an hour and a half at a distance so as not to disturb it, during which time the animal remained in an area "perhaps 500 feet on the side." The rabbit's range measured by this standard was only six acres during one and a half hours. More time may have yielded greater acreage but on the other hand accurate plotting of the area covered would undoubtedly show less acreage used. If the 6 acres actually represented home range, the home range factor was about 600.

CALIFORNIA JACKRABBIT, *Lepus californicus* Gray. — Using the same methods as for antelope jackrabbits, Vorhies and Taylor estimated 1085 California jack rabbits on 50,000 acres or one to each 46 acres. Weighing about 5.5 pounds this population density gave a per acre factor of 55 which is very evidently not an economic factor. The California jackrabbit according to Vorhies and Taylor is most abundant in the poorly grassed semi-desert part of the range which make up only a small portion of the census area.

Wooster, 1935, censused the California jackrabbit on a Kansas prairie which was more uniformly suitable to them. Counts were made by a transect survey method, a group of people marching in line 10 feet apart for one mile counting all jackrabbits flushed within the line of march. The number of people used in these drives and the number of times these drives were staged was not mentioned. One picture showed eleven persons on a drive.

During November 1939, after a drought in Kansas had become severe, 406 or one jackrabbit to about 1.6 acres were counted, and in March 1935, 484 or one to 1.3 acres.

One hundred fifty-eight were estimated per square mile in March 1933 or one jackrabbit to each four acres. As the drought in Kansas increased so did the number of jackrabbits. In November the number was about one to each 3.2 acres; in November 1934 it was one to 1.6 acres and in March 1934, one to 1.3 acres.

Wooster later, 1939, reported a common long-time number as 185 per square mile or approximately one jackrabbit to 3.4 acres. He found the average California jackrabbit in western Kansas to weigh 3039 gms., giving a per acre factor of 810 for this population level.

Factors for each population level determined by him in his earlier paper varied from 785 through 950, 1900, and up to 2340, increasing as the drought increased.

Just what happened to bring about this increase is uncertain but apparently the jackrabbits which were already utilizing the area in numbers sufficient to be indicated by the relatively large factor of 785, had either been to utilize a greater percentage of the area as drought made more extensive habitat for them, or increased so greatly that they were forced to use the area more economically than before. Whether or not all of these were economic density studies is uncertain. It is notable, however, that the factors are high.

Edge, 1935, estimating populations on the basis of general experience, found the California jackrabbit extremely rare in one oak-rose community, very little of which appears to be suitable habitat for them. His estimate was for the purpose of providing a general picture of a community and was minimum density study.

SNOWSHOE HARE, *Lepus americanus* Erxleben.—The remarkable periodic fluctuations in numbers of snowshoe hares have attracted the attention of many naturalists and the list of population studies on this species is a long one. Intensive studies on the home range and home territory are however far from common and there is little conclusive information to indicate what may be the limits of economic and noneconomic populations. Grange, 1932, followed one hare for an hour and fifteen minutes during a snowstorm which quickly obliterated old tracks, during which time, he remarks, "it could not be driven from an area perhaps ten acres in extent."

Aldous, 1937, carried on a more elaborate study between October and May by live-trapping, tagging, liberating, and retrapping hares in Minnesota. Sixty live traps were set in grid pattern, each grid being 40 acres in area.

Eight hundred and fifty-three out of 1625 tagged hares were caught at least twice. More than half the hares were trapped at their original station; almost half had moved only one-eighth mile. Aldous concluded from his data that the normal cruising radius is very small and limited to only "a few acres," conclusions drawn from more general but less intensive observation both by Klugh 1926, and Seton 1929.

More accurate measurements during many seasons and conditions still remain to be made. It is unlikely that the year long economic concentration

of this hare falls below the rate of one to four acres and perhaps not so far even during times of stress. This implies a yearly home range factor of at least 390, since adult hares in this Minnesota appear to average about 1543 gms. apiece. There comes a point at which any animal is incapable of covering greater area and still maintain life and vigor. Whether the actual minimum economic density lies in the neighborhood of this figure or above it remains to be clarified.

From this point the figures on populations reach remarkable heights which many persons have guessed, estimated and censused. Seton, 1929, estimated as many as "10,000 to the square mile" during a year of high population in certain parts of Canada. MacLulich, 1937, estimated 3,300 in one area, and 800 and 9,000 and 950 in other places.

Most studies on populations levels above the home range size are considerably smaller than those cited by Seton and MacLulich. Green and Shilling, 1934, by making a strip count, estimated 275 per square mile at the beginning of the breeding season in 1932 and 420 by banding and retrap at the beginning of the following season in Minnesota. Later, 1935, they raised the 1932 estimate to 478 and found that at the beginning of the 1933 season the number had fallen off to 374. In one square mile of their area they estimated as many as 602 hares. By the beginning of the 1936 season, they estimated only 164, a number which was less than home range capacity and therefore evidently not an economic density.

Morse, 1939, estimated about 250 per square mile during spring.

Green, Larsen and Bell, 1939, and Green and Evans, 1940, citing various previous figures mention 500 per square mile as well as most of those quoted above.

COTTONTAIL RABBIT, *Sylvilagus floridanus mearnsi* Merriam.—Dalke and Sime, 1936, tagged 113 mature and 76 immature cottontail rabbits during a period of 14 months beginning in November, using from 60 to 68 traps in a sanctuary of 471 acres. Only 49 of the immature rabbits were retrapped often enough to furnish home range data, the remaining 64 having been trapped only once or twice. Adults were retrapped from five to thirty-eight times and their ranges plotted on maps.

There was some possibility that the writers failed to catch all of the cottontails and they did not catch quite half of the 113 mature rabbits often enough to derive range data, but data for those which they did catch reveal useful information about the floor of their economic population levels.

According to the maps upon which the home ranges of these 49 cottontails were portrayed, only between 150 and 190 of the entire acres were used during the 14 months at least intensively enough to be detected by the methods employed. The density was therefore at the rate of one rabbit to from three or four acres.

It appears that Dalke's and Sime's figures represent 14 month economic densities. If so, the per acre economic factor would be somewhere between

350 and 470. This is not strictly comparable with most other census quoted above because of being based on data covering many months while others were based on instantaneous, three week and other short periods. Nevertheless we may note in passing that the factor is moderately high.

The average size of the home range was about 5.6 acres, hence overlap of home ranges amounted to at least an acre and a half and possibly two and a half acres.

It is of interest to note here that the home range factor on an average use of 5.6 acres per cottontail is only about 230 or roughly half the above economic factor. Overlap of home ranges accounts for the difference. It is also of interest that this home range factor of cottontails is not far different from the home range factors of 215 to 330 for white-tailed jack rabbits and 390 for snowshoe hares.

Wooster, 1939, was interested in a general faunal composition of a Kansas prairie, not in a study of economic densities of cottontails. His findings, achieved by cruising and observation, showed 21 cottontails per square mile of prairie without fixing the limits of the actual area which they used. The study was subeconomic in nature.

Polderboer, Kuhn and Hendrickson, 1941, were concerned only with a general picture of the faunal composition of farmland in Iowa. They estimate 35 cottontail rabbits on 160 acres of farmland on a rate of about one cottontail to four and a half acres late in the winter on an area where about 60 acres was in cornfield, presumably unplowed; 28 in sweet clover; 15 in soybean stubble; 21.5 in bluegrass pasture; and 5.5 in undisturbed weed patch and slough. The census covered took several weeks or months and revealed a concentration of rabbits which was almost as great as that of one rabbit to three or four acres discovered by Dalke and Sime. Nevertheless indications are that this was not an economic density, partly because of the purpose of the census, and partly because uninhabitable ground made up much of the census area.

Hendrickson, 1941, estimated 22 adult and 28 young cottontails on 80 acres of greatly mixed cover much of it presumably good for cottontails early in June and fifty-two adults and nearly adult cottontails in October. In other areas he spoke of two on two tracts of 17 and 8 acres in April and four per acre on the same tracts in October. The general definition of the areas indicates that they were uniformly useful to cottontails with the possible exception of 15 acres of orchard which was plowed periodically. The purpose of the study being to present a faunal picture of the diverse area described, it is not possible to compare this study fully with that of Dalke and Sime. Hendrickson's was a short-period census devoted to the summer months only.

We may note however, that the density of rabbits varied between one on three acres to one on three and a half acres on the entire 80 acre area to two and four rabbits per acre of the more uniform and smaller areas. If the 15 acres of cultivated orchard on the 80 acre area were generally useless to the cottontails, then the concentration on the remaining useful area must have

amounted to one rabbit to each 2.3 to 3 acres. In any case the concentrations were greater than those observed by Dalke and Sime and the per acre factors varying from about 400, through 470, 2800, and up to 5600, were accordingly higher. All but possibly the lowest, appear to be economic factors.

According to an earlier paper, 1936, Hendrickson had found 9 adult and 4 young cottontails on 15.5 acres during a period extending from June through July, or a concentration of one rabbit to 1.1 acres, yielding a several months per acre factor of about 2100.

Leopold, 1933, estimated the probable population of cottontails on an island in Pennsylvania at 3.5 per acre basing his estimate on observation of the numbers left after 2.5 were removed from this extensive area of good rabbit habitat.

Allen, 1938 and 1939, estimated one rabbit to 2.1 acres in Michigan by live-trapping, marking and releasing 182 individuals during the fall and winter months. Fifty-seven marked rabbits and 126 unmarked rabbits were shot, on the area during the hunting season which began in January so calculations place the total number of rabbits in the 500 acre farm at 225 individuals.

Although these figures are well above the densities found by Dalke and Sime, Allen's description of the farm and use thereof by the rabbits indicates that he was not calculating economic densities and that they lay somewhere above his figures. This censusing required about four months. It thus appears that one can have concentrations as high as one rabbit to 2.1 acres without at the same time having an economic density at that level, at least during a period as short as four months.

EUROPEAN RABBIT, *Oryctolagus cuniculus* author. — Couch, 1929, found 621 European rabbits dead on a 56 acre island after a poisoning and gassing operation; believed twice that number dead in their burrows and saw a few left uninjured by the control practice. This amounts to about 11 rabbits per acre for the entire area of the island above high tide. How much of it was not in use was not indicated but apparently only a few acres which were occupied by buildings, which would not greatly increase the concentration upward.

Such a concentration of these rabbits which appear to have been somewhat larger than cottontails, since some were descended from Belgium "hares" and Flemish giants, was marked by a noticeable degree of undernourishment. Their exact weight is not known.

SUMMARY OF PRIMARILY HERBIVOROUS SPECIES

Primarily herbivorous species maintain populations whose factors lie in the low thousands more consistently than do those of other food groups. Areal-use studies for herbivorous mice, ground squirrels, gophers and other small forms are not yet sufficiently refined to show accurately where low economic density levels lie, but such studies as are now available show that short-term (generally several weeks) per-acre factors are in excess of about 400 and from there reach into the low thousands.

General Summary

In spite of the fact that many censuses were made primarily to give a general picture of animal communities in varied vegetation types, they shed considerable light upon the numbers which mammals of different habits maintain. So, also, do many censuses, home range and home territory studies which were evidently made with the primary object of revealing economic population densities but some of which missed their mark because they were made too casually. A number of careful studies based on live trapping and release methods furnish our most substantial data.

These show that within each food class populations are a function of size. They also show that the most pure predators such as minks, weasels, coyotes, gray and red foxes do not commonly reach populations which give per acre factors in excess of 100. Their populations are such that even short term per acre economic factors are frequently only half that figure.

In contrast, and at the other extreme, the more pure leaf stem and root eating forms frequently reach such high populations as to yield factors up to 10,000 or occasionally above, although factors in the low thousands are more common and enduring. Present methods of censusing, subject to refinement which may show low economic populations to be much greater than now supposed, indicate that factors for these herbivorous species are rarely as low as 120 and generally four times as high. Refinement in censusing animals at low population levels (now the most difficult levels to census accurately) will probably show economic factors of leaf and stem eating forms much higher than now recorded. This will be accomplished by more careful areal-use studies than are now being practiced.

Illustrative of differences in population levels between relatively pure predators and relatively pure herbivores are the census of weasels by Polderboer and associates and one on cottontails by Dalke and Sime. The highest concentration of weasels, two on 5.5 acres yields a factor of 125. Between five and six acres was the average home range of a single cottontail according to Dalke and Sime and the home ranges overlap to such an extent that cottontail factors begin at the high factor of 230 and frequently reach into the low thousands. The difference between the highest short-term factor for the weasels and the lowest year long factor for the cottontails is almost twice the factor for weasels.

Species which are largely dependent upon seeds may reach such high populations as to yield factors lying in the low thousands, but economic factors frequently begin at about 90 and often do not exceed the low hundreds. By supplementing seeds with buds, they appear able to maintain moderately high factors.

Species which feed primarily upon insects, also maintain moderately high factors.

Omnivorous and insectivorous predators are able to maintain intermediate economic population levels, apparently to the extent to which they supplement their vertebrate diet with other items.

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ILLINOIS NATURAL HISTORY SURVEY,
URBANA, ILL.

Pelage Studies of Fox Squirrels (*Sciurus niger rufiventer*)

Luther L. Baumgartner

The type specimen of *Sciurus niger rufiventer* (Geoffroy) was collected by André Michaux, and his son, F. A. Michaux, both of Paris, during their travels through the wilderness of the Mississippi Valley region. This specimen, No. 556 of the Paris Museum, is described by Osgood (1907) as follows: "The entire underparts are rich ferruginous and the upper parts are of the same shade modified by a mixture of blackish; the nose and ears are not appreciably paler than the surrounding parts; the annulations of the hairs, tail, and all general markings are not peculiar." Anthony (1928) describes the color pattern as variable but usually tawny brown grizzled with gray above and pale rufous or yellowish brown below; the nose and ears are never white and the tail is mixed black and tawny rufous. Nevertheless, the writer found that the color pattern of this squirrel is quite variable in individuals taken from the same woodlot. The dorsal side commonly ranges from a dark reddish-black to a light grizzled color. The latter color is more common in the aged individuals. The color of the ventral side ranges from a bright rufous in some year-old animals; and, from dull rufous to a light grayish or dirty white in older individuals. Those with a light rufous color ventrally are relatively rare in that only three of them were handled. All of these were taken in northern Ohio. All of the data on hand, and the opinion of the late A. H. Howell (U.S. Fish and Wildlife Service) indicate that only one race (*S. n. rufiventer*) occurs in Ohio.

Color anomalies in this squirrel appear to be more or less common, as a number are reported each hunting season. It is believed that there are now records available for almost every possible radical color variation which occurs. The following variations have been authenticated.

(1) *Black Ventrally*. Two squirrels were collected in Marion county (in the same woods) which showed the following pattern: Underparts from the lower lip to anus, and extending from the right mid-lateral side to the left mid-lateral side, entirely black. The upper parts and tail normal, but with a distinct blackish cast. These were collected three miles east of Prospect, Ohio.

(2) *Black Dorsally*. On September 30, 1938, a hunter in Big Island township, Marion county, shot a squirrel that was completely black dorsally, but normal rufous ventrally. The tail was completely black. It was impossible to get the complete skin as the hunter ate the meat and threw the skin into the barnyard, where the writer was able to retrieve the tail, part of the head, a portion of the back, and almost all of the ventral side.

(3) *White Tails*. Five squirrels with white-tipped tails were examined. These were normal in every way except that the tips of the tails (from one to

three inches) were white. These were taken in the following localities: Andover township, Ashtabula county; Perkins township, Erie county; Marion county (taxidermist's shop); Coshocton county (taxidermist's shop); and Liberty township, Wood county.

(4) *Part Albinos*. A skin (in very poor condition) of a part albino was brought to the writer but there was no data as to where or by whom it was killed. The donor knew only that it came from North Central Ohio. There was no distinct pattern discernible, as the white hairs were mixed in with the normal hairs, but these white hairs were more abundant and prominent on the tail and posterior portion of the body.

(5) *Nearly Complete Albinos*. Entirely white squirrels were reported three times, but none could be examined by the writer. One was shot near Defiance, Ohio, by Christ Breckler; a second, south of Lancaster, Ohio, was shot by Tom Meyer; and the third was reported by Chalmer Burns of Darke County, Ohio.

(6) *Melanistic*. Melanistic fox squirrels were encountered but twice; once in Geauga county and once in Ashtabula county. Both skins were found in taxidermists' shops. Another was reported shot near Akron, Ohio, in 1930, but this specimen could not be located for examination.

(7) *Erythrism*. Only one case of erythrism was seen or heard of. This one skin, taken in Ashtabula county in 1932, was examined in detail. The general color was a dull red which extended over the entire body except for two small spots on the rump, the size of peas, which were normal tawny and black.

(8) *Brown Tails*. On December 17, 1937, a squirrel was trapped in Liberty, township, Darke county, Ohio, which was normal in every respect except the tail, which was uniform bone-brown (Ridgeway color key).

(9) *Normal-albino Combinations*. A resident of Washington Court House, Ohio, reported an albino fox squirrel which was uniformly white except the tail, which was normally colored. This record was later verified to me by three neighbors.

A color variation which was first thought to be abnormal is the whitish-edged tails of juveniles. The hairs on the tails of these immature animals are tipped with white which disappears as the adult pelage develops. This white-edged tail character has proved to be a reliable age character when present, but not all juveniles show it.

MOULT

The shedding of old hair and growth of new hair (moult) occurs once each year in adult fox squirrels. The moulting study was based on 31 individuals on which the moult-line was readily discernible and 18 other animals which appeared to be moulting but had no definite moult-line. In the latter the hair seemed to appear over a large part of the body at the same time, and thus the progress of the moult was difficult to analyze. From the 31 animals on which the moulting pattern was easily seen, it was possible to determine that the direction of moult was from the tip of the nose to the tail. In every case it started anteriorly and progressed posteriorly.

There appears to be a difference in time of moulting between males and females. The moulting of nine adult males occurred between March 13 and May 18, while the 23 adult females showed signs of moulting from April 24 to September 15. It appears significant that the non-breeding adult females moulted early (only one early moulting female contained embryos and these were quite small), while those females which had produced an early litter of young moulted between June and September. This is interpreted as indicating that the bearing of young retards the period of moulting.

Dates When Moulting Pattern Was Observed in Fox Squirrels

Adult Males	Adult Females
May 7, 1938	September 15, 1905 (suckling)
March 13, 1938	June 6, 1937
April 24, 1938	June 6, 1937 (not suckling—had had litter of young)
May 7, 1939	June 13, 1937 (not suckling—had had litter of young)
May 9, 1939	June 14, 1937
May 18, 1939	August 8, 1937 (suckling)
May 18, 1939	April 11, 1938 (non-breeding)
May 18, 1939	June 24, 1938 (had very small embryos)
May 18, 1939	Sept. 15, 1938 (suckling)
	April 24, 1939 (non-breeding)
	April 27, 1939 (non-breeding)
	April 27, 1939 (non-breeding)
	April 27, 1939 (non-breeding)
	April 27, 1939 (had two small embryos)
	April 29, 1939 (non-breeding)
	April 30, 1939 (non-breeding)
	April 30, 1939 (non-breeding)
	May 22, 1939 (non-breeding)
	May 24, 1939 (non-breeding)
	June 24, 1939 (had produced litter of young)
	July 6, 1939 (non-breeding)
	July 18, 1939 (had produced litter of young)

From the dates recorded for the males and the non-breeding females, it is reasonable to believe that the normal moulting period is during April and May, but that the adult females which have a litter of young during the first breeding season may not moult until two or three months later. The non-breeding females are largely the females born in the second litter of the previous year. The fact that more of them were taken in 1939 is due to the fact that an effort was made to do systematic collecting during the moulting period.

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MICHIGAN DEPARTMENT OF CONSERVATION,
LANSING, MICHIGAN.

The Life History of the Black-banded Skink *Eumeces septentrionalis septentrionalis* (Baird)*

W. J. Breckenridge

No extended study of the life history of the small lizard known as the black-banded skink, *Eumeces septentrionalis septentrionalis* (Baird) has appeared. In collecting data for a report on the amphibians and reptiles of Minnesota, the writer found this lizard widespread in the state and made an especially thorough study of this species.

An interesting account undoubtedly referring to the black-banded skink appears in Schoolcraft's "Narrative of an Expedition Through the Upper Mississippi to Itasca Lake," published in 1834 (pp. 64-65). He writes that a "small animal of the amphibious kind was here brought to our notice, under the name of Ocant Ekinabic, or legged snake, a species of lizard, striped blue, black, and white, with a disproportionate length of tail. It is thus readily distinguished from ordinary species. Its most striking peculiarity of habit, is its extreme activity and swiftness of motion." This is apparently the first mention of this lizard in the literature. The species was described and named by Spencer F. Baird in 1858, who gives "Minnesota and Nebraska" as the type locality of the species. There is some confusion in this respect, and Taylor (1935, p. 395) concludes that Fort Ripley, Minnesota, should be regarded as the type locality. Our skink is the northern form; it is replaced in the southern part of the Great Plains area by the subspecies, *Eumeces septentrionalis obtusirostris* (Bocourt).

Description

The taxonomy of the genus *Eumeces* has been dealt with exhaustively by Taylor (1935). The structural characters of Minnesota specimens agree, with minor exceptions, with his description of the subspecies. In a series of 26 Minnesota specimens the scale rows at midbody varied from 24 to 28, average 25.9; just back of anus they varied from 18 to 22, average 20.7; scales from parietal to above anus varied from 53 to 61, average 56.1. Frontonasal scale small or absent, not in contact with anterior loreal. Postnasal scale absent. Frontoparietals usually equal to or smaller than prefrontals. Maximum snout to vent length 82 mm. The following measurements are of typical Minnesota specimens:

* The present paper is a part of a thesis presented to the Graduate School of the University of Minnesota in June, 1941, as a requirement toward a Ph.D. degree. The writer wishes to express his appreciation to Dr. Samuel Eddy, Associate Professor of Zoology at the institution, for suggestions during the progress of this work, and to Dr. Karl P. Schmidt, Curator of Zoology and Dr. D. Dwight Davis, Curator of Anatomy of the Field Museum, for valuable criticism in the selection and arrangement of the material here presented.

Specimen number	1159	124	126	602	1027
Sex	Juv.	Juv.	Juv.	F	M
Total length	46	70	116	176	187
Snout to vent	24	29.5	45	67	72
Snout to foreleg	9.5	11.5	16	20	22
Tail	22	40.5	71	110	115
Length of head	6	6.5	8.5	9	10
Width of head	4.5	5.5	7	8	9
Foreleg	8	8	12.5	15.5	14.5
Hind leg	6	11	14.5	20	21
Longest toe	3.5	3.5	5.5	6	8
Axilla to groin	10	14.5	23.5	39	48

The body pattern consists of alternating stripes of light ashly olive and dark olive (Fig. 3). A median dorsal light stripe includes one-half of each scale row bordering the midline. Lateral to this in order lie a pair of dark stripes one-half scale wide, a pair of light lines a little more than one scale wide, a pair of dark lines one scale wide, a pair of white lines one-third scale wide, a pair of dark stripes one and one-half scales wide, a second pair of white lines one-third scales wide, and lastly a pair of dark lines, extending only between leg insertions, that grades into the pale yellowish or bluish of the belly. The median pair of dark lines begins well back of the nuchal scales while the light ashly of the dorsal lines extend forward over the head. The other lines extend forward to the eye. All lines merge on the distal half of the tail. Labials, chin, throat, soles of feet, anal border, and sometimes a chest patch yellowish, except spring males which have bright salmon-orange about jaws. Limbs dark above and bluish gray or yellowish beneath.

The southern subspecies, *E. s. obtusirostris* (Bocourt), differs from *E. s.*

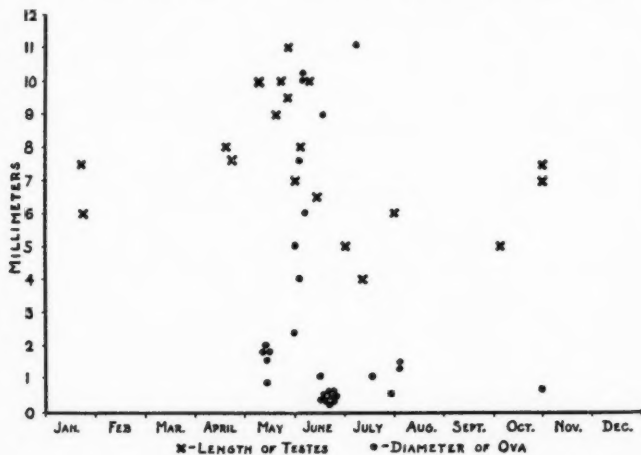


Fig. 1. Seasonal size variation in the testes and ova of the black-banded skink.

septentrionalis (Baird), in having the frontonasal scale large and in contact with anterior loreal, the frontoparietals larger than prefrontals, and in the strong tendency for the median pair of dark stripes to be lost. *E. fasciatus* (L), the only other skink found in this area, is distinguished from *E. s. septentrionalis* by the presence of a postnasal scale, the extension of the bifurcating median light line onto the top of the head, and the presence of five rather than seven light stripes on the body.

Young are shiny black with seven light longitudinal stripes of a yellowish color. Top of head black, dorsal light lines disappearing on neck. The two outermost light stripes on either side normally narrower and more sharply defined than the three dorsal ones. Both labial series, chin, and throat yellowish. Lower sides and belly pale bluish. Tail in newly hatched individuals deep brilliant blue, becoming progressively duller with age, the blue color disappearing in individuals of about 50 mm. snout to vent length.

The sex of adult skinks is easily determined in spring when the malar regions of the males are bright salmon-orange. This color is lacking in females at all seasons. Heads of adult male skinks are usually recognizably larger than those of females. The average head size of 21 males was 10.3 mm. wide and 11.5 mm. long; while that of 20 females was 9.1 mm. wide and 10.4 mm. long. The width was taken just anterior to the ear openings and the length from posterior point of interparietal to the anterior tip of nasal scale. The proportionate size of the heads is best presented in the proportion, body length into head width plus head length. This varies in 14 females from .268 to .303; while in 14 males it ranged from .290 to .346. With only three exceptions in this series of 28 specimens those below .300 were females and those above were males. No significant differences in head measurements of the sexes could be found in the first and second year animals.

Range

E. s. septentrionalis occurs rarely in southern Manitoba and commonly southward through eastern North Dakota and South Dakota, Minnesota, western Wisconsin, Iowa, and eastern Nebraska and Kansas (Fig. 8). In extreme southern Kansas and throughout Oklahoma it intergrades with *E. s. obtusirostris* (Bocourt) which extends on southward across eastern Texas (Taylor, 1935, p. 404 and 409).

Habitat

A statement concerning the habitat of the black-banded skink in Iowa is made by Ruthven (1910, p. 205-6); Burt remarks on the habitat in Kansas (1928, 63-66); and a few brief notes relative to its habitat in general appear in Taylor's monograph of the genus *Eumeces* (1935, p. 65, 402).

The writer, working exclusively in Minnesota, found the black-banded skink a secretive animal only rarely encountered active on the surface of the ground. The skinks spend most of their time in small excavations beneath sticks, stones, bark, boards, or pieces of tin or paper. The most productive hunting for them is done with a strong hook for turning over such objects, especially those that have been lying undisturbed for some time and have

settled well into the surface of the sod. The excavations made by the lizards often connect with small burrows which are deepened in the fall when more protection is needed and certain of these undoubtedly are further deepened for use as hibernating quarters.

At least in the northern part of its range this skink appears to require a comparatively soft soil allowing it to burrow to a sufficient depth for successful hibernation; warm, slightly moist, well drained situations for nesting; and habitat conditions supporting a population of orthopterons and arachnids. Gravelly glacial deposits and their accompanying sandy outwash provides these conditions in Minnesota and appear to be the limiting factors in the distribution of this lizard within the state. It has been recorded from 33 of the 87 Minnesota counties (Fig. 8). It is significant that the animal has not been recorded in either the southeastern or northeastern regions. To the south and east of Minneapolis the surface soils are largely the fine dense clays of the Pre-Wisconsin glacial drifts together with extensive loess deposits. Both of these soils are markedly more dense and less suited to the burrowing habits of the skink than are the Middle and Late Wisconsin deposits and the extensive sandy outwash plains to the west and northwest of Minneapolis. In the northeast the repeated glacial scourings have left the Pre-Cambrian rocks entirely exposed or very thinly covered with drift. Here the absence of skinks is evi-

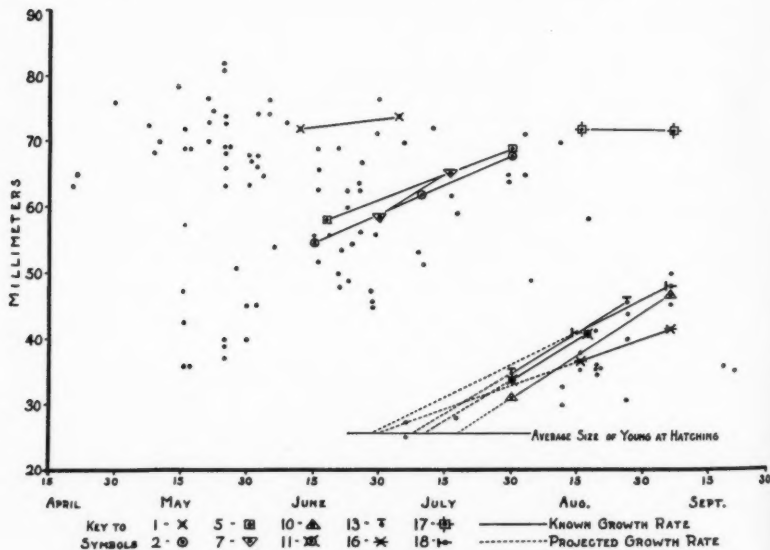


Fig. 2. Data on the rate of growth of black-banded skinks in the wild.

dently due to these soil conditions and not to temperature, since their range extends much farther north into Manitoba in the favorable sands and gravels farther west.

Hibernation

The date of suspension of activity in the fall for the black-banded skink has not been satisfactorily determined, but the animals apparently become dormant rather early. Through September it became increasingly difficult to locate skinks in favorable habitats and none was found after the middle of the month in the wild, although captive animals were seen active on warm days until late October. Several were unearthed from hibernation on October 31, 1939. It is probable that they congregate and remain active near their winter retreats during warm fall days as do snakes, finally retiring permanently sometime during October.

Some data were secured regarding the location and nature of hibernation quarters. Mr. Joe Eheim of Hutchinson, Minnesota, reported a single skink unearthed on January 24, 1939, from beneath two feet of frozen gravel along a stream bank. The following winter, October 31, 1939, two groups of three and eight animals were taken at a depth of about three feet in the same gravel bank. Since these were secured only incidentally by a gravel digging crew and no efforts made to locate more animals, these individuals may have represented only part of the skinks from larger numbers hibernating in compact groups. This probability is suggested by Scott and Sheldahl's (1937, p. 192) observation in Palo Alto County, Iowa, reporting a mass of 52 black-banded skinks unearthed from a gravel deposit at a depth of four and one-half feet on February 15. Late in the fall the writer confined seven skinks in a screen cage 2' x 2' x 4' in which four types of soil were available to the animals. Six of the seven were found to have burrowed in the sand to varying depths, but only those two that reached the screen bottom, 12" deep, survived the winter.

The data at hand show that in central Minnesota the skink emerges from hibernation in late April. Specimens were collected under natural conditions as early as April 19. One of the skinks that survived experimental hibernating conditions emerged April 29. All the animals taken in April proved to be males, females not appearing until well along in May.

Breeding Habits

There is a definite enlargement of the testes in the male during the spring (Fig. 1), although this is not as marked as in the birds. Measurements were taken only of adult specimens 65 mm. or more in body length. Testes from 8 specimens taken between May 1 and June 15 averaged 9.3 mm. in length, while those of 4 specimens taken June 15 to July 30, averaged 5.4 mm. in length. The minimum seems to be reached in late summer, with size recovery well started in the hibernating animals.

On the same graph data are presented showing that the ova are still at their minimum when the females emerge from hibernation. Very rapid enlargement occurs after fertilization and continues until the eggs are laid. The ovaries then remain dormant throughout the winter.

Mating occurs in the black-banded skink immediately after the appearance of the females from hibernation in late May. Vigorous adults, captured on May 21 and 22, 1939, and placed together in confinement, copulated readily a number of times on May 22, 24, and 26. Deane Mather reported a male skink actively pursuing a female at Lake Alexander in Morrison County, on June 2, 1937. Both were collected and were found to be in full breeding condition. As many adults were taken within the period May 15 to June 15 as were taken throughout the remainder of the year. This very likely is a direct result of their breeding activities. Records for the immature animals are much more evenly distributed throughout the summer.

The following description of the copulation was written at the time the observations were made. The male, in beginning to show an interest in the female, arched his tail upward from the hind legs, letting the tip drag. On one or two occasions he stiffened the tail almost erect from the base. He followed her about, nosing her body and nudging her for perhaps ten minutes. Finally he grasped the skin of her shoulder just over the right front leg and held on tenaciously. With his body lying along her right side, the male

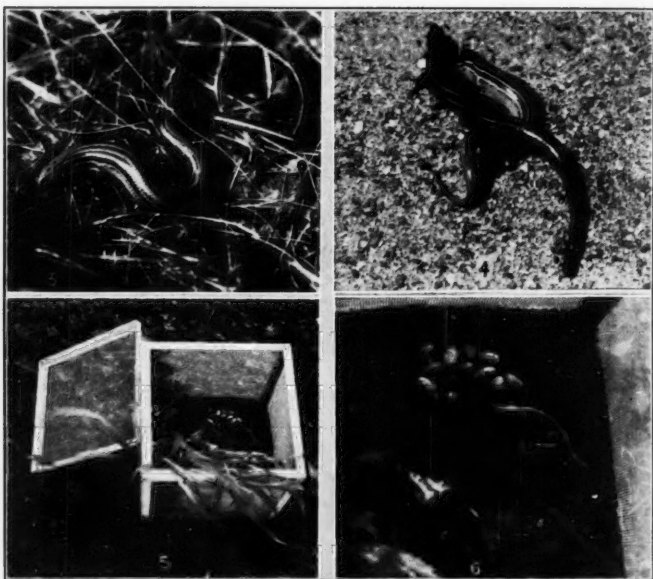


Fig. 3. Typical markings of black-banded skink. Fig. 4. Copulating pair of black-banded skinks. Fig. 5. Female black-banded skink guarding eggs in experimental cage. Small triangular piece of wood completely covering the nest has been removed. Fig. 6. Closeup of fig. 5.

encircled the female's body just ahead of the hind legs with his forelegs. He then curled his tail around under her body from the right side in such a way that their cloacas met. Their tails in this position crossed at right angles (Fig. 4). For about two or three minutes they lay quiet except for jerky, sidewise movements of the tail of the male at about one second interval. The female remained quiet and made no effort to dislodge the male. After they separated the female crawled away while the male lay motionless. Copulation was observed six or eight times, and each time it was essentially as described above. This courtship and mating behavior is almost identical with that described by Noble and Bradley (1933) for *Eumeces fasciatus* and *E. laticeps*, except that the male "vibrated the end of his tail" in the eastern species, instead of arching it as in *septentrionalis*.

One unsuccessful attempt at copulation resulted in the male's hemipenes being extruded but not inserted in the cloaca of the female. Each hemipenis opened out in a two-lobed, almost flower-like structure, from one side of the vent and was about one-half inch across. The basal limbs of the organs were reddish, each surmounted by a wide, convoluted, fleshy, flange-like structure which was reddish basally with a grayish-yellow cordlike structure on the convoluted margin. This marginal structure appeared jelly-like in texture. The organ remained erect for about two minutes.

Egg Laying and Nesting

The period between the time of copulation and egg laying was determined approximately in the case of two females. Females no. 19 and no. 20 were last bred on May 26. They were then segregated in small cages (Fig. 5) which were placed inside the large rearing cage. The small cages were investigated at intervals of a few days, until sets of eggs were found on July 4, which were laid between June 25 and July 4. Assuming that the eggs were laid July 1, the period between the last mating and oviposition would be 35 days in both cases.

The eggs of the black-banded skink (Fig. 6) are elliptical in shape and of varying shades of dirty white to buffy color. The outer coating is tough and leathery, the texture of the surface being much like the upper surface of a mushroom, not sticky but only very slightly moist. They are surprisingly large for the size of the females laying them. The following measurements of 36 eggs of 5 different sets were taken at the time of laying:

Number of eggs	Size in mm.
1	7.0 by 12.5
2	7.0 by 13.0
1	7.5 by 12.0
1	8.0 by 12.0
2	8.0 by 12.5
13	8.0 by 13.0
2	8.0 by 14.0
8	8.0 by 15.0
1	8.5 by 12.0
1	8.5 by 14.0
2	9.0 by 12.5
2	9.0 by 13.0

The extremes in width were 7 mm. and 9 mm.; the extremes in length, 12 mm. and 15 mm. The average size of these eggs was 8.0 mm. by 13.4 mm.

The complete set of eggs is laid within a period of a few hours and but one set is laid per year.

The six records obtained relative to the time of egg laying ranged from June 25 to July 17. That eggs may be laid as early as the middle of June is suggested by the finding of eggs in the oviducts of two females taken June 5 which averaged respectively 10 x 6 mm. and 10 x 7 mm.

Seven captive females laid sets consisting respectively of 5, 7, 7, 8, 8, 11, and 12 eggs. The numbers of well developed eggs in the oviducts of females collected in the field were as follows: 5, 7, 8, 9, 9, 11, 11, 11, 11, and 13. Two sets of eggs found in the wild each contained 7 eggs. The number of eggs laid by this species was found to vary from 5 to 13, the average of 19 records being 8.79 eggs per set.

Like the eggs of snakes, those of skinks absorb moisture during incubation and become distinctly larger before hatching. Three eggs were measured about midway in the incubation period:

Length in mm.	Width in mm.
15.0	10.5
16.0	9.7
16.0	10.0
Just previous to hatching, these three eggs measured:	
17.0	10.0
17.0	10.0
18.0	11.0

The average of 7 eggs just before hatching was 10.6 mm. by 18.0 mm.

The eggs of captive skinks were invariably laid in excavated cavities just under small stones, pieces of wood or bark. A nest found in the field by L.

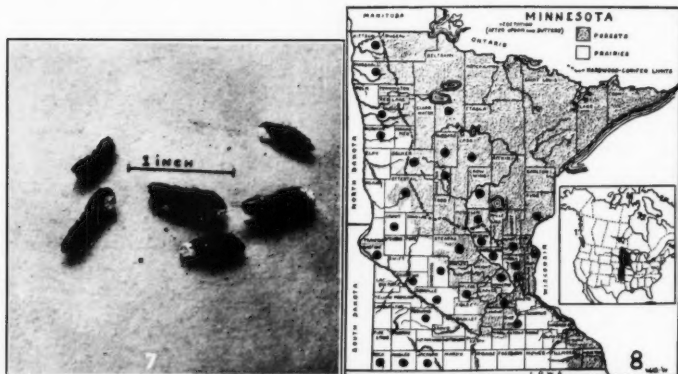


Fig. 7. Typical droppings of black-banded skink. Fig. 8. Map of known range of black-banded skink.

Koelnau was under a small, flat stone only slightly imbedded in the ground, and one reported by George Rysgaard was under a small log. This type of situation provides the eggs with a reasonably moist atmosphere while they are still protected from excessive wetting during heavy rains. In this connection female no. 20 hollowed out a cavity an inch or so down in the sandy soil beneath a small board. Females no. 19 and no. 17 both kept their eggs in small hollows directly beneath the boards. Other than this, their situations seemed identical. The deeper nest of no. 20 always seemed more moist than the other nests and this one failed to hatch while those of the other two were successful.

Female skinks remain constantly in attendance at the nests during the incubation period (Fig. 6). This probably serves to protect the eggs from enemies but it has also been suggested that the females move the eggs about according to moisture and temperature conditions. Eggs were found moved several inches at times but this movement was not found to correlate with these factors. Noble and Mason (1933) suggest that the female skink's habit of sunning and returning to the eggs adds heat and speeds the development of the embryos.

The above described nest locations go far toward equalizing temperature extremes during incubation as shown by the following temperature records of a single nest:

August 13, 1938.	Outside temperature	3:00 p.m. 91° F. in shade.
	Nest cavity temperature	3:00 p.m. 80° F.
	Outside temperature	7:45 p.m. 85° F.
	Nest cavity temperature	7:45 p.m. 80° F.
August 14, 1938.	Heavy rain about 4:00 p.m. brought the outside temperature of 94° F. down to 72° F. in the evening.	
	Outside temperature	7:00 p.m. 74° F.
	Nest cavity temperature	7:00 p.m. 80° F.
August 15, 1938.	After the heavy rain of the previous afternoon.	
	Outside temperature	5:30 a.m. 67° F.
	Nest cavity temperature	5:30 a.m. 75° F.
August 17, 1938.	After a very cool night.	
	Outside temperature	5:30 a.m. 62° F.
	Nest cavity temperature	5:30 a.m. 70° F.

Incubation Period

Skinks are cold-blooded animals and consequently the incubation period of their eggs varies with the temperature. This period has been approximately determined for 6 sets of eggs. These were hatched in screen-covered cages where the light and heat reaching them were reduced and this may have lengthened the period. In the following list it is assumed that the eggs were laid midway between the dates indicated:

Set No.	Eggs laid between	Hatched	Approx. Inc. Period
4	July 4-July 17	August 20	40 days
6	July 4-July 16	August 22	42 days
10	July 4-July 17	August 26	46 days
14	July 4-July 17	August 24	44 days
17	July 7-July 9	August 30	52 days
19	June 25-July 4	August 19	49 days

The average of these 6 records is 45.5 days for the incubation period of the skinks in captivity. Set no. 17 was most accurately determined as being 52 days, which was probably within 2-3 days of the actual period for this particular set.

Hatching

It appears from the data just given relative to the hatching of eggs in captivity that the latter part of August is the normal hatching period for this species in this latitude. Data derived from skinks in the wild suggest different conclusions.

Capture dates and sizes of five very young animals follow:

Animal No. 10 taken July 31, size 31 mm.
Animal No. 11 taken July 31, size 34 mm.
Animal No. 13 taken July 31, size 35 mm.
Animal No. 16 taken Aug. 16, size 37 mm.
Animal No. 18 taken Aug. 15, size 41 mm.

The table on page ?? gives the known rates of growth of these individuals. Calculation based on these data give the following approximate hatching dates:

Animal No. 16—June 28
Animal No. 18—June 29
Animal No. 13—July 4
Animal No. 10—July 18
Animal No. 11—July 12

Using the average incubation period determined as 45.5 days, these data strongly support the suggestion made previously that some eggs are probably laid early in June.

On the other hand, skinks of 35.5 mm. and 36 mm. body length, were taken on September 7. Utilizing the average growth rate of .37 millimeter per day for immature animals (as shown later), these would have hatched about August 5. Thus it appears that the breeding and egg laying season for these animals must each extend over a period of at least a month to result in the appearance of newly hatched young over a period of the same length, although the choice of nesting sites, admitting greater or lesser amounts of heat to reach the eggs, may result in considerable variation in incubation periods.

Growth Rate

Taylor (1937, p. 67) using a size group method, arrived at an age of nine years for 65 mm. specimens of *E. fasciatus*, a species identical in size with *E. septentrionalis*, giving roughly 4.5 mm. as the annual growth increment. Noble and Mason (1933) found captive young *E. fasciatus* grew 4.5 mm. in 55-59 days. The following data indicate that these growth rates are probably far too slow for skinks living in the wild.

The growth of skinks kept in captivity over periods of several months during 1938, and fed on insect sweepings, was so slight that the writer was led to conclude that the above workers' calculations were probably correct. These data were discarded after growth records were obtained from marked animals living in the wild the following year.

A well populated habitat was located during the spring of 1939 in the dry, sandy, oak savannah in southern Anoka County. Several years previously a load of metal scraps, rocks and rough chunks of concrete had been strewn about on the thin blue-grass sod. These had remained undisturbed and a small thriving colony of skinks had developed there in an area perhaps 100 feet in diameter. These materials could be readily lifted and the animals captured. The objects were then replaced, the skinks marked and liberated for future capture. This colony remained intact during the summer of 1939 and considerable data were secured. A system of clipping toes was devised for individual identification and 23 animals were marked and liberated in this limited area. The graph (Fig. 2) shows the complete record of 123 captures indicating the date and snout to vent length of the animals at the time of capture.

In the lower right portion of this graph, an isolated group of records of small animals appears in the late summer. An upward trend in body length during the late summer months is evident in this group. The following figures show the actual growth in body length recorded over certain time intervals and the calculated growth rates of 5 first year animals:

Animal	Growth Period	Increase	Growth rate mm. per day
18	21 days	7 mm. (41-48)	.33
16	21 days	5 mm. (37-42)	.24
13	27 days	11 mm. (35-46)	.41
11	16 days	7 mm. (34-41)	.44
10	37 days	16 mm. (31-47)	.43

These data give an average growth rate for animals in this size class of .37 millimeters per day.

The lines connecting the various symbols on the graph indicate growth rates for individual animals as recorded on various dates. This group represents the growth of the newly hatched skinks up to the time of suspension of activity in the fall. The fact that the individual growth lines found in this group parallel each other so closely and follow the general trend of the group shows that these records represent a reasonably accurate average growth rate for animals during their first season. The appearance of 35 mm. and 36 mm. young in September 19 and 22 is a strong indication that some eggs may hatch as late as the middle part of August. Similarly, the appearance of 36 mm. animals after hibernation on May 16 and 17 is further proof of this same fact.

Further growth data were obtained on three animals in the size class over 50 mm. in body length:

Animal	Growth Period	Increase	Growth rate mm. per day
2	45 days	13 mm. (55-68)	.29
5	42 days	10 mm. (58-68)	.24
8	15 days	6 mm. (59-65)	.40

From these data, the average growth rate for animals over 50 mm. in body length is found to be .31 millimeters per day. This indicates a decrease in the growth rate of larger animals. The central group of lines on the graph connecting symbols no. 2, no. 5, and no. 7, also paralleled each other and

follow the general trend of the records in the middle group. Since the early records in this group are in the same size class as the first year animals when they went into hibernation, there seems little doubt but that this group represents the second year skinks.

The adult animal no. 1 grew but 2 mm. over a period of 25 days (72-74). Adult no. 17 (72 mm.) was recorded as making no growth over a period of 22 days. These scant data agree with the natural inference that the growth rate is rapidly reduced as the animals approach the maximum size for the species.

The writer feels that this graphically represented growth series serves as a substantial basis for the statement that black-banded skinks grow to mature size (65 mm. and larger) at the end of their second year of life and are ready to breed the following spring.

The tails of newly hatched skinks are about equal to the snout to vent length, while in adults they approach twice that length. Correspondingly, the following rates of tail growth produce an average growth rate of .73 mm. per day, a little over twice that of the average body growth rate for first and second year animals collectively, .34 mm. per day.

Animal	Growth Period	Increase	Growth rate mm. per day
10	37 days	32 mm. (34-66)	.86
11	17 days	14 mm. (41-55)	.82
13	27 days	23 mm. (41-64)	.86
16	21 days	10 mm. (45-55)	.48
18	21 days	13 mm. (54-67)	.62

Some data were secured regarding the rate of growth of regenerating tails. The following pertain to this growth in wild skinks:

Animal	Growth Period	Total Growth	Growth rate mm. per day
4	4 days	Merely scabbed over
20	10 days	Round tip, approximately 2 mm.	.20
1	23 days	8 mm.	.35
2	45 days	25 mm.	.56
5	42 days	42 mm.	1.00

After the breaking off of a tail, several days are necessary for the wound to heal and growth to begin after which time the growth soon accelerates to about that of normal growth. No. 4, captured after only 4 days, had the wound merely scabbed over. No. 20, after 10 days, had developed only a blackish, hemispherical tip to the broken member, probably between 1 and 2 mm. in length. The tail of no. 1, after 23 days, had grown sufficiently to bring the rate up to .35 mm. per day, while no. 2 and no. 5, over periods of 45 and 43 days, has still further increased the average rate to about that of a normal tail.

Food

The stomach contents of 37 skinks collected in the field were examined. These specimens came from a wide variety of localities in the state and were taken throughout their active season. The data secured from this source are

presented in Table no. 1. H. E. Milliron and H. D. Pratt of the Division of Entomology, University of Minnesota, identified the materials listed. A wide range of food appears, but there is a definite choice of crickets, grasshoppers, and spiders. Orthoptera constitute 27.3% (by frequency of occurrence) of the diet while Arachnida make up 29.5%. Homoptera (mainly leafhoppers), Coleoptera, and Lepidoptera (largely larvae), are distinctly second choice food animals, and make up 28% of the diet. The fact that ants, a particularly available form, were found in but one stomach is striking. One case of cannibalism was noted.

The second type of food data was secured from examination of the droppings of captive animals which were kept for a number of months in an outdoor, partially sunken, screened cage. The droppings were compact, elongate, and tipped with the white of the solid uric acid waste characteristic of bird droppings (Fig. 7). These animals were fed on sweepings in which it was thought a wide range of small insects would be available. These results differed considerably from the foregoing data. Here the Orthoptera, consisting almost entirely of crickets, and the Homoptera, consisting of the leafhoppers and fulgorids, make up almost the entire diet.

The first type of food data from animals collected in the field undoubtedly gives the better picture of the normal diet of these skinks.

Enemies

Several specific records of animals preying on adult skinks were secured. In Grant County on April 21, 1939, a striped ground squirrel, *Citellus tri-decemlineatus*, was found eating an adult male black-banded skink. The specimen was freshly killed and the stomach contained food indicating that it had been taken after emergence from hibernation.

A road-killed specimen of the western hog-nosed snake, *Heterodon nasicus*, taken in Norman County, September 19, 1939, contained an adult skink. This record suggests that both the hog-nosed snakes, *H. nasicus* and *contortrix*, as well as *Thamnophis radix*, and *Coluber c. flaviventris*, all of which frequent the drier habitats favorable to skinks, might be significant enemies of this lizard.

Scales of skinks have been identified in the pellets of marsh hawks, *Circus hudsonius*, taken in Anoka County.

Theodore Nordquist had opportunity to observe repeatedly with a strong telescope a pair of nesting sparrow hawks near Minneapolis and reported that numerous skinks were fed to the young.

Richard Voth reported from near Dassel, Minnesota, a skink pinned on the thorn of a black locust tree within a few feet of the nest of a migrant shrike, *Lanius ludovicianus migrans*.

Blakemore (1940, p. 22) found skink remains in barred owl, *Strix varia varia*, pellets taken in Glenwood Park in Minneapolis.

Giles (1940, p. 381) records remains of Eumeces (undoubtedly *E. septentrionalis*) in fecal samples from raccoons, *Procyon lotor*.

Cannibalism does occur in this lizard since a female, no. 541, taken in the wild at Minneapolis, July 18, 1937, contained a young skink in her stomach.

Summary

1. The black-banded skink is known to occur in 33 Minnesota counties. It prefers sandy or gravelly habitats, being absent on the dense loess and clay soils of southeastern Minnesota, and the stony red clays and Pre-Cambrian rock outcrops of northeastern Minnesota.

2. In central Minnesota skinks become largely inactive in September, going into permanent hibernation late in October. Males emerge from hibernation late in April or early in May, while the females do not appear until later in May.

3. Mating occurs late in May and early in June.

4. Sexes may be distinguished in adults during the breeding season by the fact that the male has the malar regions salmon-orange; at other season the larger head of the male is a reliable distinction in nearly all cases.

5. Six sets of eggs were laid between June 25 and July 17. Nineteen records of egg clutches varied from 5 to 13, the average per clutch being 8.79.

6. Thirty-six eggs of 5 different sets at time of laying had width extremes of 7 and 9 mm., and length extremes of 12 and 15 mm., average 8.04 by 13.37 mm. A definite expansion of the eggs occurs during incubation.

7. Nests are placed invariably in small excavations beneath boards, stones, bark, or similar cover.

8. Approximate incubation periods for six sets of eggs hatched in captivity varied from 40 to 52 days, the average being 45.5 days. The females remain with the eggs nearly all of the time during incubation.

9. Twelve newly hatched skinks varied from 24 to 26.5 mm. in body and head length, average 25.5 mm.

10. Five marked animals during their first season in the wild grew on an average of .37 mm. per day; three second year animals, .31 mm. per day; while adults grew much more slowly.

11. Skinks are of mature size (65 mm. or over in body length) at the beginning of their third season.

12. The western hog-nosed snake, *Heterodon nasicus*, marsh hawk, *Circus hudsonius*, and the striped ground squirrel, *Citellus tridecemlineatus*, were recorded as feeding on adult skinks, while adult skinks were found to prey on young of their own species. The barred owl, *Strix varia varia*, the sparrow hawk, *Falco sparverius*, the migrant shrike, *Lanius ludovicianus migrans*, and the raccoon, *Procyon lotor*, have been reported preying on this lizard.

13. Food analyses of 37 wild skinks collected throughout the season indicated their food to consist of the following major items on frequency of occurrences:

Orthoptera	27.3%	Homoptera }	
Arachnida	29.5%	Coleoptera }	28.0%
		Lepidoptera }	

TABLE 1.—Stomach Analyses of 37 Black-banded Skinks
(Individual animals in each stomach)

[illegible]

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Growth and Feeding of Newborn Price's and Green Rock Rattlesnakes

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On August 9th, 1941, a 429 mm. female green rock rattlesnake, *Crotalus lepidus klauberi*, collected in Carr Canyon, Huachuca Mountains, Cochise County, Arizona, gave birth to four young, three males and one female. At 12 noon, when they were first found, three had already been born, but the fourth did not emerge until an hour later. All were irritable from the first, promptly broke the membranous sacs in which they were enclosed and struck violently at any passing object. All were marked and colored much like the adults except that the delicate pink along the venter of the latter was not in evidence; and the tails, which in the adult are salmon or terra cotta red (including the basal segment of the rattle) were brilliant sulphur yellow for at least their distal half and the pre-button of the rattle.

There was no trace of an egg tooth, reported by Gloyd (1937) in embryos of this species. In total length they averaged 190.5 mm., measuring respectively, 182, 182, 198, and 200 mm. Between August 17th and 19th, all shed their skins, becoming somewhat more brilliant in color.

Nine days later, on August 18th, six young were born to a female Price's rattlesnake, *Crotalus t. pricei*, measuring 455 mm., collected in the Chiricahua Mountains, Cochise County, Arizona. These had all been born and had broken out of the membranes when they were discovered at about 10 o'clock in the morning. All were alive and active. Like the above species, they were replicas of the adults in pattern, with the color less intense. These also lacked an egg tooth. They averaged 163 mm. in length, their individual lengths being 159, 160, 160, 164, 165, and 170 mm. From August 24th to 26th all shed their skins, becoming more contrastingly colored and differing from one another in shade. Two obvious types of ground color were noted, one distinctly brown and the other decidedly gray. One specimen, the largest, was brown; two were quite gray; and the others were somewhat intermediate. Unlike the *klauberi* young, these were decidedly gentle, never offering to strike or otherwise displaying nervousness—a temperamental difference noted in the "wild-caught" adults of the two species.

The two broods were placed together in a glass terrarium measuring 10 by 20 inches and 12 inches in height. Five large pitted rocks, slag from an iron smelter, provided natural resting places and crevices into which the snakes could retire; "sheet" moss, such as is used by florists for decorative purposes, for the floor of the terrarium and between the rocks, and two small cacti, constituted the entire setting. A round clay dish, 3 inches in diameter and an inch and a half deep, was used for water.

The terrarium was kept in a room where the temperature was almost con-

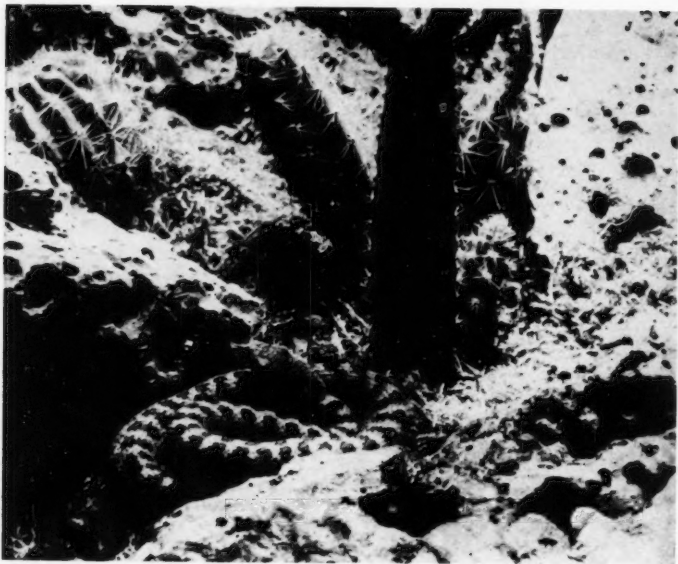


Fig. 1. Newborn *Crotalus triseriatus pricei*, photographed in a terrarium.

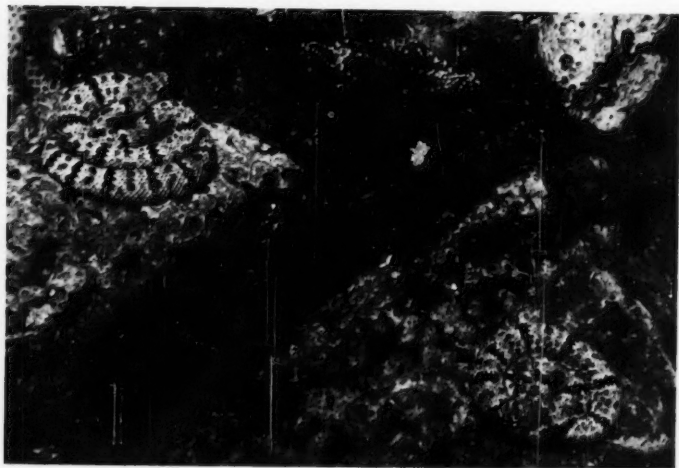


Fig. 2. Newborn *Crotalus lepidus klauberi*, photographed in a terrarium.

stantly at 80°, but additional heat and light were provided by a 70 watt electric light bulb, which shone directly into the terrarium through its wire screening top, for nine or ten hours each day. This increased the temperature in the terrarium from three to eight degrees above that of the room. The snakes coiled on the rocks immediately under the light, from six to eight inches from it, where the temperatures were highest. The heat provided by the light also aided in maintaining a lower relative humidity during the late summer, probably more nearly approaching natural conditions.

The time of greatest activity was usually in the late afternoon and at night. Activity was partly influenced by feeding, becoming more prolonged as digestion became complete, and as the time for the next meal approached. Conversely, activity was reduced after feeding, and was least at midday. This is interesting in view of the fact that temperatures and light were far more constant, and all factors less variable than they would be in a natural state.

Feeding

Fourteen days after the birth of the young of *Crotalus lepidus klauberi*, both broods were offered portions of a small mouse cut up into six pieces. This method of offering pieces of adult mice had been employed successfully in feeding the young of *C. horridus*. Only one hind quarter was taken, probably by one of the *klauberi*. An attempt was made to feed both broods similar portions of adult fence lizards, (*Sceloporus undulatus*), but these were refused, as were repeated offerings of pieces of mice. Among other items of food refused were mealworms, small grasshoppers, earthworms, and later salamanders (*Plethodon cinereus* and *Desmognathus f. fuscus*). A hatchling ring-neck snake, *Diadophis punctatus edwardsii*, lived in the same terrarium and mingled with the rattlesnakes, but was unmolested during several weeks. Although they showed great curiosity in everything placed in their quarters, they were distinctly repelled by salamanders, gliding away frantically if they happened to come in contact with them. They showed no interest in salamanders dead or alive. A small king snake, *Lampropeltis multicincta*, was placed in the terrarium to find whether the king snake would attack the rattlesnakes, and whether the rattlers would assume their characteristic defense posture. The king snake showed no sign of recognition of the rattlesnakes' presence, and the latter displayed only curiosity, actually approaching the king snake and making a minute examination of him. Subsequently, this king snake took small *Sceloporus* readily. On one occasion, a newborn water snake was quickly presented after the king snake had taken a lizard. It was seized but immediately released. The king snake ate a second lizard without hesitation, while the water snake lay close by unnoticed.

Three weeks after the birth of *klauberi*, hatchling *Sceloporus undulatus* and *Anolis carolinensis* were offered with success. It was expected that lizards would be accepted because adults of both *klauberi* and *pricei* fed upon them eagerly. Although they showed no preference for one species of lizard over another, the long tails of the anoles were a source of obvious annoyance. Subsequently only *Sceloporus* were given.

In a natural state they would encounter *Sceloporus*, principally *jarrovi*. This may be an example of "predator-prey" synchronization, the young of the species preyed upon being born at approximately the same time as the young of the predator. Thereby a supply of food proportional in size becomes immediately available for the young rattlesnakes, and a mechanism of selection and control of the more numerous and more prolific species. As the two species grow, they probably remain more or less proportional both in numbers and in size.

The fact that the eggs of *Sceloporus undulatus* in the pine barrens of New Jersey hatch from late August into October made it possible to obtain a supply of lizard food nearby. Weekly collecting of hatchling *Sceloporus* reached a peak on the 26th of September with 35 lizards taken in eight hours. No lizards were found after October 23rd. The adult lizards, which were hunted with equal assiduity, became less frequent as the young became more numerous with the lowest ratio less than 1 to 10. These observations were substantiated in the same general region by Mr. Asa Pittman's collecting, whose services were enlisted in accumulating a food supply for the young rattlers.

The problem of maintaining a large number of food lizards was solved by freezing them, covering them with water to prevent desiccation, and storing them in a frozen state in ice cube trays in the freezing compartment of a refrigerator. Hundreds of lizards could be obtained months in advance and stored in a small space. This eliminated the problem of feeding the lizards and losses from their deaths. No doubt the danger of parasites being transferred from lizard to snake is materially reduced by freezing. When needed to feed the snakes, a "cube of lizards" could be thawed quickly with hot water and offered to the young snakes, which never hesitated to accept them even after the food had been frozen for months. Adult lizards similarly preserved were taken by the adult Price's rattlesnakes, and the small lizards were used also to feed the young *Lampropeltis multicincta* mentioned before.

Although food is usually taken from a forceps, the young snakes find the dead lizard during their peregrinations, and eat it forthwith. I have frequently seen one of them sense the lizard immediately on coming upon it, and after a few flicks of the tongue, seize and begin to engulf it. At first the lizards were offered alive. The rock rattlesnakes usually bit and released the prey, death ensuing very rapidly. In one instance, a lizard was struck while clinging to the side of one of the rocks, dropped instantly to the floor of the terrarium and did not move again. On another occasion, two snakes of the same species struck simultaneously at the same lizard, both missed but one snake struck the other in the lower part of the eye. A small spot of blood at the site of the wound was visible for some days, but no further injury resulted. A similar occurrence under identical circumstances resulted in one of the Price's rattlesnakes biting another in the middle of the back, but no reaction at all was noted. This species usually seized the lizards and proceeded to swallow them or held on until their struggles ceased, then either dropped them and sought the head to begin the swallowing, or shifted them around in the mouth without releasing

them, often starting hind end first or at a leg. Sometimes the food was swallowed doubled up, with the greatest of difficulty. Even after some weeks there was still a tendency for the young *pricei* to seize a dead lizard, when presented on a forceps, with the same violence as if it were alive. Soon after all food was offered dead it was accepted with greater readiness. Living lizards seemed to frighten certain individuals so that they startled the others by their frantic thrashings about, and thereby created general confusion.

Over a period of 118 days these snakes consumed 207 *Sceloporus*, ranging in length from 55 to 90 mm. and weighing from 1 to 2 grams each. They were fed on an average of once each week. It was impossible at first to distinguish what individual snakes consumed, so that records show that all ten snakes consumed 56 lizards in addition to 20 taken by the *C. l. klauberi* alone, and 131 by the *C. t. pricei* alone. It was soon noticed that one individual of each species was not feeding. Attempts were made to induce natural feeding. When these failed the specimens were preserved. Two more of the rock rattlesnakes soon ceased feeding, after the second shedding of the skin, so that the records of food consumed by this species are mostly of one snake, the largest of the brood, a consistent and voracious feeder. The remaining Price's rattlesnakes fed without interruption.

The surviving male rock rattlesnake, grown to 260 mm., was offered the head of a freshly killed adult mouse on October 23rd. He struck at it while it was held in a forceps, and proceeded to swallow it after it was released; a hind quarter and the sacrum of the same mouse were taken eagerly on the same occasion. Thereafter this snake fed entirely on mice. New born and very young rats and mice were secured, killed when they reached the proper size, and frozen into cubes in the same manner as the lizards. There was no difference in the readiness with which the frozen food was taken as compared with freshly killed food. The mice weighed on an average of 3 to 3½ grams, but once or twice mice of 6 grams and over were taken. Two or three mice of average weight were sufficient for one meal. At first this snake displayed a decided preference for mice with hair, but soon the naked young of both rats and mice were accepted.

Three of the Price's rattlesnakes were gradually induced to take very young mice, but they were only accepted if entirely hairless. The whiskers of the older mice apparently were a source of irritation. When the snakes seized the snout of the mouse, they would quickly draw away, giving every evidence of having been discouraged by the tickling of the hair. If the mouse was seized at the rear, or by a leg, deglutition proceeded smoothly.

Digestion was quite rapid, defecation taking place on the second or third day after feeding, and usually again on the fifth day. With most snakes of the various species under my observation, I have found that feces are voided twice, on the average, per feeding; the first usually within a week of the feeding. There are evacuations of uric acid from time to time which may be confused by the novice with feces. Storer and Wilson (1932: 171) say in

reference to *Crotalus v. oreganus*, "It is evident that feces are not passed after each feeding, but only at long and irregular intervals." This is entirely contrary to my experience. It is well known among reptile keepers in zoos that feces are passed soon after feeding and that this can be noted throughout a large collection within a week after a general feeding. The snake mentioned by the above authors that ate 17 rats totaling 1,446 grams in 264 days and voided feces only once, was a remarkable creature indeed. A moment's consideration of what these figures imply indicates the impossibility of such a feat.

Assimilation was remarkably complete in the young rattlesnakes under discussion. Although feces were always black masses distinct from the solid, white, uric acid passed with them, parts of the food animal were seldom distinguishable, except for hair in the case of the mouse-eating *C. l. klauberi*. I was unable to find even lizard scales, usually present in the feces of adults.

All these snakes drank frequently, both from the dish provided for that purpose and from the pits in the rock when water was spilled into them. The Price's rattlesnakes particularly liked to drink water as it trickled over the rocks, as they probably do in the natural state. Storer and Wilson (*op. cit.*) gave their captives *no water*, having estimated that their food contained sufficient moisture to fill their needs; but it is well known that snakes, almost without exception, drink water in captivity.

It will be remembered that although the young Price's rattlers were marked and colored essentially like adults, the green rock rattlers differed from adults in that the tail was sulphur yellow for two-thirds of its length, including the button, and not terra cotta red. It was observed that distinctive behavior is associated with this conspicuous caudal coloration. In several species of snakes, notably of the genera *Agkistrodon* and *Bothrops*, the grub-like, bright colored tail of the young is said to function as a lure for prey. The juvenile rock rattlers wave their tails with a slow peristaltic motion in close imitation of the movement of certain insect larvae. Meanwhile, the body would lie coiled and perfectly still, blending with the rocks on which they lay, leaving the tail to "crawl" along as an apparently distinct entity. The illusion was excellent. It is conceivable that a lizard chancing upon so tempting a morsel would rush to seize it, only to be met by the fangs of the snake. That this must happen in a natural state is likely, but I have been unable to associate feeding, or hunger, with this behavior. Tail-waving was indulged in by all the *C. l. klauberi*, never by the *C. t. pricei* in which the tail is not distinctively colored. No particular design could be noticed in this action. It might take place immediately after the snakes had been fed, or when no lizard was in sight, or when it could not have been seen by the lizard, even if there were one in the general vicinity. On several occasions when a snake was seen to be waving its tail, a lizard was placed in the cage, but proved to be too much disturbed by being handled to be tempted by food, real or otherwise. Living lizards offered when the snakes were hungry were seized without preliminary tail-waving. The lizard was always pursued or struck as soon as it came within reach. Tail-waving was not observed while the snakes were moving about, but only when they were coiled

and at rest, when it might be continued without interruption for as long as half an hour. The tail-waving became less and less frequent as the snakes grew older. It was observed only once during the fourth month and thereafter not at all. With each successive molt the yellow of the tail became less pronounced, and after the fourth molt showed definite signs of becoming red like that of the adults.

Some authors have interpreted the tail movements of captive snakes as luring behavior. Henry (1925) describes the young of the hump-nosed viper, *Akgistrodon hypnale*, as having whitish tails that undulated when lizards (skinks) were placed in the cage. In view of the fact that the lizard, which seemingly induced the reaction in the snake, was not eaten until sometime after it was placed in the cage, it seems unlikely that the tail of the snake acted as a lure, especially as there seemed to be lizards in the cage at all times. It has not yet been shown conclusively that the tails of such heterochromous-tailed snakes function as a lure.

Growth

Growth of the young rattlers was uniform except for the specimens that refused to feed. The single rock rattlesnake that fed well, a male, was the longest at birth, measuring 200 mm. In 118 days this snake grew 112 mm., 56 per cent of its original length, and attained a weight of 18.5 grams. The parent snake measured 429 mm. Klauber (1937) gives the minimum size of gravid females of this species as 390 mm. During a period of 43 days, the young snake consumed 37 grams of young and half-grown mice; previous to that, at least 20 grams of lizards were taken. The first molt took place 9 days after birth. Thereafter the skin was shed at intervals of 47, 49, and 51 days, the clouded condition of skin and eyes preceding ecdysis lasting eight to ten days. The skin was always shed perfectly, and the rattle acquired three well-formed segments in addition to the button, one at each molt after the original postnatal ecdysis.

One specimen in the rock rattlesnake brood, the only female and the smallest of the brood, was constantly restless, shed only once, and was never observed to feed voluntarily. This specimen was given one or two force feedings. In spite of this it increased 32 mm. in length, though becoming very emaciated. The thriving male was the least, the female the most irritable of the brood. Klauber estimates the length of *C. l. klauberi* at birth to be 195 mm.—5 mm. more than the average for our brood.

The six young Price's rattlesnakes thrived with the exception of one individual whose history was much the same as that of the female *C. l. klauberi* just mentioned. This specimen was one of the smallest of the brood, and did not feed, but increased 28 mm. in length. It molted only once, a week after birth. In the first 135 days of their life, the remaining five normal snakes increased in length, on the average, 98 mm., from the average length of 163 mm. at birth. The greatest increase was in the specimen largest at birth: from 170 mm. to 280 mm. Their weights increased to an average of 11.62 grams.

At least 300 grams of lizards were consumed in that time, and about 20 grams of mice.

Ecdysis took place a week after birth, and thereafter three times at intervals of 40-44, 34-39, and 45-62 days. The last record is for only two snakes; the others had not yet become opaque 60 days after the third molt. The opaque period preceding ecdysis lasted six to eight days. Without exception the skin was sloughed in one piece, and a new segment was added to the rattle at each molt except the first, which merely frees the button of the prebutton (Klauber: 1940). Two specimens, of this species, of a brood of five, in the collection of the American Museum of Natural History (A.M.N.H. 63616-7) were born August 3rd, 1941, to a female collected near Safford, Cochise County, Arizona. They were preserved about one month after birth and probably had not been fed during that time. The condition of the rattle indicates that they sloughed the skin only once. They measure 200 and 202 mm., nearly 40 mm. more than the average for our brood at birth. Klauber (1937) estimates the average size of the new born as 175 mm. The smallest specimen he examined was 170 mm.—the maximum of our brood. Considerable initial growth is apparently possible without food.

The growth data thus obtained from captive specimens agree closely with Klauber's computations for other rattlesnakes, as do all the pertinent data obtained from these captives. This is somewhat contrary to Klauber's statement that "studies of rattlesnake growth cannot be based on captive specimens, since growth is distorted by artificial conditions."

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Geographical Variation of Ventral Markings in Toads

Albert P. Blair

In any relatively sedentary organism with a wide distribution, local variation is to be expected since (1) with a limited local population the production of new characters through mutation cannot be expected to be the same for all localities (at least within a limited time interval), (2) even if the same mutant genes should appear in all localities they would be preserved in some and lost in others merely by chance, (3) even though the same mutant genes should be preserved in all localities their respective frequencies would vary from locality to locality by chance, (4) natural selection will favor different genes or gene constellations in different environments, and (5) in different parts of its range the species may come in contact with different closely-related species, the results of this contact (introgressive hybridization, etc.) making for a different range of variation. The efficacy of each of these factors in the production of genetically distinct local populations is dependent upon the degree to which the organism tends to be migratory or fixed in habit.

To some extent the data from local variation studies may be used as indirect evidence of the size of breeding units. In general, a high degree of local differentiation may be taken as indicative of small breeding units, and, conversely, the absence of local differentiation may be taken as evidence of a continuous interbreeding population without division into local units. The literature on local variation indicates that the latter condition is extremely rare.

Materials and Methods

In a previous paper¹ the writer considered local variation in body size, foot size, parotoid gland width and parotoid gland length in *Bufo americanus*, *B. terrestris*, *B. fowleri* and *B. woodhousii*. The present paper is concerned with variation in ventral markings in 23 populations of *B. fowleri*, 14 populations of *B. americanus* and six populations of *B. woodhousii*. The 48 series consist of 43 collections of adult male toads and five collections of adult female toads. The series vary in size from 10 to 551 animals. Twenty contain 40 or more toads and 17 contain less than 20 toads. The smaller series can be used to advantage if one keeps in mind the limitations imposed by their size. Where a collection from a locality contained animals intermediate in structure between two species the same procedure as utilized previously (Blair, 1941) was followed: if the two species concerned were known to occur in the locality the intermediates were not considered; if, however, only one species was known to occur in the locality the apparent intermediates were taken as part of an interbreeding population and were considered.

¹ Blair, Albert P. 1941—Variation, isolating mechanisms, and hybridization in certain toads. *Genetics* 26:398-417.

The toads under consideration show wide variation with respect to ventral markings, ranging from unmarked (except for the black throat of the male) to heavily reticulated venter. Between these extremes are the single pectoral spot and various other degrees of spotting. The addition of spots other than the pectoral spot always proceeds from anterior to posterior; if, for instance, one-half the venter is spotted it is always the anterior one-half which is involved. With respect to their ventral markings toads were classified on an arbitrary scale from 1 to 6: (1) venter unmarked, (2) pectoral spot only, (3) spots on anterior one-third of venter, (4) spots on more than one-third and not more than two-thirds of venter, (5) spots on more than two-thirds of venter, and (6) venter reticulated. Such a classification, though obviously less precise than mensuration, involves a high degree of objectivity. No effort was made to distinguish between intensity of markings, as between a light pectoral spot and a dark pectoral spot.

Local Variation in *B. fowleri* Males

With the exception of three animals from Jena and one from Holly Springs, all toads fall within the first three classes. Of the 23 series, seven have the first class as the mode, 11 the second class and five the third class. The series from Elizabeth Islands and Lakeville have class 1 as the most populous group; such differences as exist between the two may well be due to the small size of the samples. The next two localities, Jones Beach and Flushing, are somewhat less than 200 miles from the Massachusetts localities. These insular series resemble one another and differ from the Massachusetts toads in that animals with pectoral spot only form the largest class. The differences between Jones Beach and Flushing are probably significant. The Wheeling series is small but seems indicative of a range of variation somewhat similar to that of the New York localities; inasmuch as all toads have pectoral spot only a rather homogeneous population is suggested. The next four collections — Nashville, Bloomington, Vincennes and Olney, all within a radius of 60 miles — are alike and resemble the New York insular series in that toads with pectoral spot only form the predominant class. It is to be noticed that the Nashville and Bloomington series, from localities only 15 miles apart, show differences which must be considered significant in view of the size of the series. The three Oklahoma series are alike in that ventrally unspotted toads constitute the most numerous class in each. The Scraper and Wilburton series have the three classes arranged 1-2-3 in order of magnitude but differ as to the percentage of animals in each of the three classes. The Garvin series has the three classes 1-3-2 in order of magnitude. The significance of this difference may be questioned since the series contains but 18 toads. It is to be noted, however, that the Fulton series, from a biotically similar locality 75 miles farther down the Red River, shows a very similar distribution. Of the next six series from Texas, Louisiana, Mississippi and Alabama, five have class 3 most numerous, a condition not heretofore encountered. In view of its size the exceptional Vicksburg series cannot be taken as very significant. The Benton, Alabama, series is definitely different from the group of series just

considered and resembles the New York and Indiana-Illinois series. The next three series, from Georgia, South Carolina and North Carolina, have the same mode as the Benton series. The North and South Carolina series have the order of magnitude of the three classes represented 2-1-3, as in the Benton series; in the Georgia series, however, the order is 3-1-2.

Local Variation in *B. americanus* Males

Of the 14 series, nine have the third class as the mode, two the fourth class and three the fifth class. In general the series show greater variability than the *B. fowleri* series; seven contain representatives of five of the six classes. Toads with more than two-thirds of the venter spotted form the largest class in the series from Utica. The New Jersey and Pennsylvania series differ from the Utica toads in having the mode at class 3 with class 4 almost as large; they differ from one another in that toads of class 5 are proportionately better represented in the Pennsylvania series. The Oshkosh toads show the most extensive ventral markings of any of the series under consideration, with 19% of the animals having reticulated venters and an additional 58% with more than two-thirds of the venter marked with spots. The small Pinckney and Winona Lake series have modes at class 5 and class 4, respectively. Of the remaining eight series in Indiana, Missouri, Arkansas and Oklahoma, seven have class 3 as the mode. The Tulsa series (23 specimens) has class 4 as the mode. It is again to be noted that Nashville and Bloomington differ as to percentage distributions in the various classes although having the same mode. Considering all the *B. americanus* series, it is of interest that the most extensive ventral markings are found in toads from northern localities.

Local Variation in *B. woodhousii* Males

The collections are less representative of the range of the species than are those for *B. fowleri* and *B. americanus*; all are from the eastern part of the range. The range of variation is similar to that of the *B. fowleri* series. Four of the six collections have class 1 as the mode; the two series with class 2 as the mode are small and the mode might conceivably shift to class 1 with more specimens. The significance of the absence of class 3 in the Onawa series is questionable.

Comparison of Variation in Males and Females

Data on the few adequate series of female toads available indicate that the ventral markings of females may differ considerably from those of males of the same population. For instance, the Tulsa *B. woodhousii* females have class 2 as the mode while the males have class 1. The Bloomington female *B. fowleri* have the same mode as the males but there is a much greater representation of class 1 in the males.

Comparison of Species

With the exception of four animals, all of the 1,709 male *B. fowleri* from 23 localities have ventral markings which fall within the first three classes. The

VENTRAL MARKINGS IN TOADS

Males

		N	1	2	3	4	5	6	Mean
<i>♂ B. fowleri</i>	Elizabeth Ids., Mass.	11	11						1.0
	Lakeville, Mass.	30	27	2	1				1.1
	Jones Beach, N. Y.	100	15	68	17				2.0
	Flushing, N. Y.	47	16	29	2				1.7
	Wheeling, West Va.	11		11					2.0
	Nashville, Ind.	115	3	67	45				2.4
	Bloomington, Ind.	551	103	399	49				1.9
	Vincennes, Ind.	34	13	19	2				1.7
	Olney, Ill.	15	6	7	2				1.7
	Scraper, Okla.	169	126	34	9				1.3
	Wilburton, Okla.	48	24	14	10				1.7
	Garvin, Okla.	18	11	1	6				1.7
	Fulton, Ark.	16	8	2	6				1.9
	Stevens Creek, Tex.	74	17	8	49				2.4
	Woodville, Tex.	31	8	5	18				2.3
	Jena, La.	88	16	19	50	3			2.4
	Vicksburg, Miss.	11	7	1	3				1.6
	Holly Spgs., Miss.	40	10	10	19		1		2.3
	York, Ala.	23	4	6	13				2.4
	Benton, Ala.	204	60	138	6				1.7
	West Point, Ga.	53	5	27	21				2.3
	Modoc, S. C.	15	6	7	2				1.7
	Elon College, N. C.	25	8	16	1				1.7
		1729							1.9
<i>♂ B. americanus</i>	Utica, N. Y.	30		3	6	9	12		4.0
	Leonia, N. J.	76		8	30	25	11	2	3.6
	Polk, Pa.	44		1	17	16	10		3.8
	Oshkosh, Wisc.	108			2	20	64	22	5.0
	Pinckney, Mich.	11		1	2	3	5		4.1
	Winona Lake, Ind.	19		2	4	7	4	2	4.0
	Nashville, Ind.	59	1	4	48	5	1		3.0
	Bloomington, Ind.	300	30	29	138	62	41		3.2
	Princeton, Mo.	13		1	7	3	2		3.5
	Blue Spgs., Mo.	10			8		2		3.4
	Imboden, Ark.	11		2	7	1	1		3.1
	Winslow, Ark.	46	3	4	22	10	7		3.3
	Tulsa, Okla.	23	1	1	7	9	5		3.7
	Wilburton, Okla.	25	3	4	12	3	3		3.0
		775							3.6
<i>♂ B. woodhousii</i>	Onawa, Ia.	19	13	6					1.3
	LaMine, Mo.	30	15	11	4				1.6
	Choteau, Okla.	12	5	6	1				1.7
	Inola, Okla.	15	4	9	2				1.9
	Tulsa, Okla.	170	96	54	20				1.5
	Waynoka, Okla.	10	7	2	1				1.4
		256							1.6

Females

		N	1	2	3	4	5	6	Mean
♀ <i>B. fowleri</i>	Jones Beach, N. Y.	50	1	41	8				2.1
	Bloomington, Ind.	90	4	72	14				2.1
	Scraper, Okla.	16	1	14	1				2.0
		156							2.1
♀ <i>B. americanus</i>	Oshkosh, Wisc.	22					15	7	5.3
	Bloomington, Ind.	67	7	4	26	20	10		3.3
		89							4.3
♀ <i>B. woodhousii</i>	Choteau, Okla.	30	3	22	5				2.1
	Inola, Okla.	19	1	17	1				2.0
	Tulsa, Okla.	82	19	48	15				2.0
		131							2.0

Key to grading system: (1) venter unmarked, (2) pectoral spot only, (3) spots on anterior one-third of venter, (4) spots on more than one-third and not more than two thirds of venter, (5) spots on more than two-thirds of venter, and (6) venter reticulated. N is number of specimens in series.

four exceptional animals come from the central Gulf Coastal Plain, a region which has toads best referred to *B. fowleri* but which have the appearance of being a fusion product of *B. fowleri* and *B. americanus*. While the *B. fowleri* populations have ventral variation restricted to the first three classes, the mode may fall at any of the three classes.

The *B. americanus* series show a greater range of variation in ventral marking. The mode may fall at class 3, 4 or 5. It will be recalled that the central Gulf Coastal Plain *B. fowleri* are unique among *B. fowleri* populations in having the mode at class 3, a fact consistent with the thesis that these toads represent a fusion product between *B. fowleri* and *B. americanus*.

Ventral variation in *B. woodhousii* males is like that in *B. fowleri* in that all animals fall within the first three classes. Four of the six modes fall at class 1; the remaining two, which fall at class 2, are for small series.

One might be led to the conclusion that ventral markings are of value as a species differential between *B. americanus* on the one hand and *B. fowleri* and *B. woodhousii* on the other hand, since from the data it would seem that almost any toad found in the eastern half of the United States would be *B. americanus* if it falls within class 4, 5 or 6. This might be true were it not for the fact that there has been a considerable amount of hybridization between the members of the *americanus-terrestris-fowleri-woodhousii* complex of toads. Such being the case, the application of a specific designation to a given individual must rest upon consideration of the sum total of characters of that animal.

Discussion

The present data would seem to indicate neither a lack of local differentiation nor a high degree of local differentiation, but an intermediate situation which is probably true of the vast majority of plant and animal forms. Collections of toads from localities in the same general area tend to resemble one another. For instance, *B. fowleri* from four localities in southern Indiana and Illinois are alike in that animals with pectoral spot only form the mode in each instance. While collections from the same area usually resemble one another, they may differ significantly. A distance of only 15 miles separates the toads from Nashville and Bloomington, yet the two populations show significant differences. It is perhaps correct to think of the toads under discussion as animals with sufficiently localized breeding units that populations 10-20 miles apart may differ significantly, but not sufficiently localized that populations 2-3 miles apart may differ. While populations 10-20 miles apart may differ, the facilities for gene dispersal are such that populations several hundreds of miles apart may show resemblances.

ACKNOWLEDGMENTS

The writer is indebted to the Department of Herpetology of the American Museum of Natural History for making available the toads of the Elizabeth Islands and Leonia series, and to Mr. Robert Mathewson for the Utica and West Point series. For other series not collected by the writer acknowledgment has previously been made (Blair, 1941). Prof. Th. Dobzhansky and Dr. John A. Moore very kindly read the manuscript and made suggestions.

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Hermaphroditism in *Carunculina parva*, a Fresh Water Mussel*

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In 1898, Victor Sterki published the results of a study of sexuality in fresh water mussels in which he recorded the occurrence of a single individual of *Carunculina parva* which contained "a goodly quantity of sperm besides ova in abundance." In this early mention of hermaphroditism in this species, no details regarding the nature of the individual gonad follicles are recorded. At a later date Utterback (1916:165) wrote of *C. parva*: "Hundreds have been collected in nearly all the northwest Missouri lakes and streams, but not a single one has been found without the marsupial character of the gills and the sexually dimorphic female shell. However the male and female shells appear in central Missouri." Here again no further details are given, and it seems conclusive that Utterback's statement was based on an examination of the secondary sexual characters and did not involve analysis of the gonad tissues.

The present writer has been unable to locate any other direct reference to hermaphroditism in *C. parva*. In the description of this species in Baker's Mollusca of Wisconsin (1928:253), the author cites Utterback's statement that *C. parva* is "locally hermaphroditic" but adds no further comment.

The availability of a series of young stages of *C. parva* in the Salt Fork of the Vermilion River near Homer, Illinois, gave opportunity to study the gonads of this species in considerable detail. On June 23 and June 30, 1942, collections were taken which formed the basis of the present study. Five individuals varying in shell length from 12 mm. to 21 mm. were carefully removed from the shell and were fixed in alcohol-formol-acetic killing solution. These mussels were small enough to be embedded entire and sectioned serially at a thickness of 8 or 10 microns. They were stained in Heidenhain's iron hematoxylin.

A preliminary study revealed that the gonads of all five specimens of *C. parva* contained both eggs and spermatozoa. On closer observation it was found that the hermaphroditic condition was not one of complete balance, with equal proportions of male and female follicles, but that in every case the ovarian follicles far outnumbered the male follicles. In all the specimens the gonad tended to show a division into a large posterior-ventral region composed wholly of ovarian follicles and a much smaller anterior-dorsal region composed of sperm-bearing follicles. In Figure 1, although the orientation of the section is not perfect, male follicles are observable on the right of the photograph and female follicles on the left.

* A contribution from the Zoological Laboratory of the University of Illinois, Urbana, Illinois.

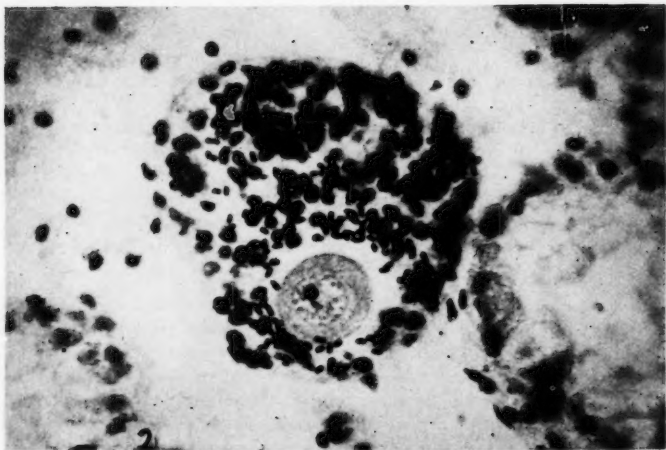
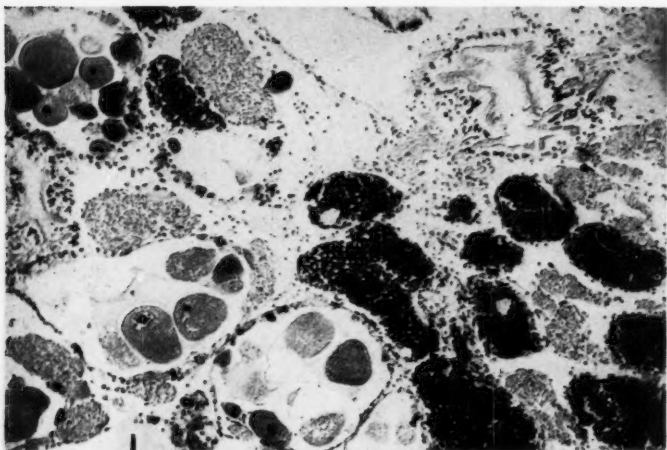


Fig. 1. Section through a typically hermaphroditic gonad of *Carunculina parva*, showing male follicles to the right and female follicles at the left. The gonad duct, in section, shows near the upper right of the photograph. Magnification, about 100 diameters.

Fig. 2. Section through a preponderantly male follicle containing a single egg. Magnification, about 575 diameters.

Contrary to the findings of van der Schalie and Locke (1941), in their studies of *Anodonta grandis* and *A. imbecillis*, in four of the five individuals of *C. parva* under observation some follicles were found containing products of both sexes. Only one reference to the occurrence of hermaphroditic follicles has been found in the literature. Bloomer (1939:297) recording the results of studies on *Anodonta cygnea*, a European species, states:

An examination of the sections of the gonads. . . has not, with some doubtful exceptions. . . revealed male and female products in the same acinus—usually each acinus produces either spermatozoa or ova.

The doubtful exceptions are:—in some individuals, parts of the sections made during the autumn and winter months have what appear to be degenerate ovarian products and sperm morulae, sometimes sperm as well, in the same acinus; in several River Frome individuals. . . parts of the sections show one or more ova nearly if not quite encircled by spermatozoa and sperm morulae, and in one section spermatozoa and sperm morulae in the center of ovarian products.

A typical example of the hermaphroditic follicles found in *Carunculina parva* is shown in Figure 2, a photograph of a section through a predominantly male follicle bearing fully mature sperm and a single egg. This particular follicle was located far toward the anterior-dorsal part of the gonad tissue and lay in contact with other male follicles and with the posterior lobes of the liver.

In most instances it was observed that the eggs enclosed in male follicles were smaller (20-24 microns) than eggs from strictly female follicles (40-100 microns). The eggs in essentially male follicles were free from the germinal epithelium, and their small size does not seem to indicate relative immaturity. Both eggs and spermatozoa appeared mature in all the individuals, which would seem to indicate that this hermaphroditic condition does not represent a phase in a periodic sex reversal.

The author wishes to thank Professor H. J. Van Cleave of the University of Illinois for the invaluable advice and criticism offered throughout these studies. Dr. Henry van der Schalie very kindly identified the mussels which formed the basis of this study.

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Survival Time of Trout in Relation to Occurrence¹

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The occurrence and distribution of trout have been the subjects of considerable investigation and much more speculation. The physical factors usually accredited with determining their existence include dissolved oxygen, free carbon dioxide, temperature and pH, but there is little agreement as to which may play the most important rôle.

More is known of the culture, distribution, and physiological limitations of the brook trout than any other species of trout. The rainbow and the brown trout have also been studied but to a lesser extent. Few, if any, tests have been made of the three species under similar conditions with the purpose of obtaining experimental data which would aid in accounting for their distribution and interspecific relationships.

The brook trout is considered a "head-water" form and usually occurs in the upper stretches of trout streams where, it is said, conditions are most favorable for its existence. The rainbow and brown trout, when present, occupy a position in the stream, as a rule, below that of the brook trout, but usually with an overlapping of ranges.

Trout distribution in the Great Smoky Mountains National Park was investigated by surveys made on about 75 streams, comprising a total of approximately 300 miles of water. Brook trout (*Salvelinus fontinalis fontinalis*) and rainbow trout (*Salmo gairdnerii irideus*) are numerous in all except a few of the park streams. The average upper elevational limit of rainbow trout is 3502 feet. The average lower limit of brook trout is 3289 feet. The difference, 213 feet, represents from 1 to 1½ miles of stream.

In these fast mountain streams oxygen is present to the point of saturation, and carbon dioxide is present only in minimal amounts independent of the elevation. The highest temperature at which the two named species were found to occur was 78° F. for the rainbow trout and 66° for the brook trout. The pH range for rainbow was 6.1 to 7.0, for brook trout 4.7 to 6.9.

These observations revealed differences in habitat which were thought to have a bearing on the occurrence of the two species, but their interpretation did not seem to furnish an answer in many cases. The next step was to subject these trout to various experimental conditions in the nature of survival tests, with the hope that the results so obtained could be correlated with the field

¹ The material presented is a portion of a thesis submitted as partial requirement for the degree of Master of Science, Department of Zoology, University of Cincinnati, June, 1941.

observations and a more nearly complete and satisfactory explanation derived therefrom.

Materials and Methods

The object of the experimental study was to obtain quantitative survival values for the three species of trout, brook (*Salvelinus fontinalis fontinalis* Mitchell), rainbow (*Salmo gairdnerii irideus* Gibbons), and brown (*Salmo trutta* Linnaeus), when subjected to various environmental conditions having a bearing on their relative hardiness or physiological limitations. The most significant physical factors operating in the natural environment of trout which could be reproduced and controlled in the laboratory were chosen for these tests.

The experimental work was carried on at the park headquarters building, Great Smoky Mountains National Park. Fingerling trout, 2½ to 3 inches in length and 3 to 4 gm. in weight, were supplied by the Park Service. For each test fish were chosen as nearly as possible of the same size and weight. Both homotypic and heterotypic groups were tested under most of the experimental conditions. The cessation of all movement was used as the criterion of death. Open-topped battery jars or sealed bottles were used as containers for the fish according to the requirements of the experiments.

Temperature, pH, free carbon dioxide, half bound and fixed carbonates, and dissolved oxygen determinations were made at definite intervals during each test. Dissolved oxygen concentration was determined by the Winkler method, and the free carbon dioxide, half bound and fixed carbonates, by a modified Seyler technique. Colorimetric methods* were used for determining pH values within the range 3.8 to 9.6. Beyond these limits the pH, when referred to, was calculated from the normality of the solution. The containers were kept in a cold water bath except when the reaction to high temperature was being tested.

Survival tests were made with the fish under each of the following conditions:

- Exp. 1. Straight survival (All conditions supposedly normal at the start).
- Exp. 2. High temperature (Other conditions normal at start and not changing enough to be important in result).
- Exp. 3. Low oxygen tensions (Other conditions normal at start and not changing enough to be important in result)
- Exp. 4. High carbon dioxide tensions (Other conditions normal at start and not changing enough to be important in result).
- Exp. 5. High alkalinity (Other conditions normal at start and not changing enough to be important in result).

* These data are given in the more extensive tables included in the thesis previously mentioned.

Exp. 6. High acidity (Other conditions normal at start and not changing enough to be important in result)

Exp. 7. High concentrations of NaCl (Other conditions normal at start and not changing enough to be important in result)

In the different experiments the methods used and types of data obtained varied according to the nature of the particular test. For example, in the first straight survival test each species was placed in a battery jar containing 6 liters of fresh creek water which was obtained from a nearby stream supporting trout. Data were recorded as given in the following table. Temperature is given in degrees Fahrenheit, dissolved oxygen, free carbon dioxide and half bound and fixed carbonates are expressed in parts per million.

Exp. 1. Straight Survival—Tests 1a, 1b, 1c (Homotypic grouping)

	(a) Brook	(b) Rainbow	(c) Brown
	20 fish 90 gm.	20 fish 88 gm.	21 fish 60 gm.
Length of exp.	165 min.	120 min.	150 min.
Temperature change	69°-73°	72°-75°	72°-75°
Change in pH	6.6-5.5	6.5-5.5	6.5-5.6
Free CO ₂ (at start)	5.78	7.79	11.56
Free CO ₂ (1st death)	24.63	25.64	23.63
Free CO ₂ (50% survival)	26.89	28.40	25.64
Free CO ₂ (at finish)	28.40	29.66	26.50
H. B. & F. CO ₂ ¹ (at start)	7.43	6.9	9.74
H. B. & F. CO ₂ (1st death)	7.94	7.43	9.33
H. B. & F. CO ₂ ¹ (50% survival)	8.46	7.43	10.5
H. B. & F. CO ₂ (at finish)	8.2	7.94	9.33
D. O. ₂ (at start)	9.32	8.97	8.76
D. O. ₂ (1st death)	2.38	2.57	3.55
D. O. ₂ (50% survival)	2.28	2.47	3.18
D. O. ₂ (at finish)	2.50	2.72	3.08
1st death	105 min.	75 min.	105 min.
50% mortality	135 min.	90 min.	135 min.
Total mortality	165 min.	120 min.	150 min.
Average length of survival	138 min.	97 min.	135 min.

1 Abbreviation for Half Bound and Fixed Carbonates.

2 Abbreviation for Dissolved Oxygen.

In the second test somewhat different methods were employed. Smaller numbers of fish were used and the three species were placed in the same container, which in this case was a gallon bottle. The water analyses were made before the fish were added and after the last mortality.

Exp. 1. Straight Survival—Test 2 (Heterotypic grouping)

	Brook	Rainbow	Brown
Length of Exp.	138 min.	3 fish	3 fish
	Start Finish	13 gm.	12.5 gm.
Temp. change	68°-73°		
pH change	6.9-6.3		
Free CO ₂	9.8-35.19		
H. B. & F. CO ₂	12.3-13.07		
D. O.	9.13-3.83		
1st death	120 min.	83 min.	72 min.
50% mortality	120 min.	102 min.	77 min.
Total mortality	138 min.	103 min.	95 min.
Average length of survival	126 min.	96 min.	81 min.

In determining the effects of high temperature the apparatus was so arranged that the fish received a continuous supply of well aerated water. Samples were tested at intervals to make certain that the dissolved oxygen remained high and the carbon dioxide low. The temperature was increased slowly by means of a water bath from a starting point of about 70° F. to a high of 86°. The rate of rise was about 2° per 10 minutes. The following table illustrates the nature of the data recorded during each test.

Exp. 2. High Temperature—Tests 1a, 1b, 1c (Homotypic grouping)

	(a) Brook	(b) Rainbow	(c) Brown
	20 fish	20 fish	21 fish
	58 gm.	59 gm.	59 gm.
Length of Exp.	90 min.	150 min.	105 min.
Temperature change	73°-86°	69°-85°	73°-85°
pH change	7.9-7.7	7.1-7.5	7.9-7.7
Free CO ₂ (at start)	6.03	7.29	3.52
Free CO ₂ (1st mortality)	5.13	6.03	5.53
Free CO ₂ (50% mortality)	6.54	6.54	4.02
Free CO ₂ (total mortality)	7.29	5.53	4.02
H. B. & F. CO ₂ (at start)	21.01	13.32	21.27
H. B. & F. CO ₂ (1st mortality)	22.3	21.01	21.01
H. B. & F. CO ₂ (50% mortality)	22.04	21.53	21.01
H. B. & F. CO ₂ (Total mortality)	22.55	22.55	21.01
Temperature of 1st distress	82°	81°	83°
Temperature of 1st mortality	84°	83°	84°
Temperature of 50% mortality	85°	85°	85°
Temperature of Total mortality	86°	85°	86°
D. O. (at start)	7.69	8.82	7.65
D. O. (1st mortality)	7.13	6.60	7.1
D. O. (50% mortality)	6.79	7.00	7.1
D. O. (Total mortality)	7.16	7.16	7.1

Low oxygen tensions were produced by boiling the water. By this method oxygen content as low as 1 p.p.m. could be produced. The desired tensions were arrived at approximately by mixing fresh creek water with that which had been boiled. By this method, however, it was difficult to duplicate a certain oxygen content in successive tests. The results of a sample test are given in the following table.

Exp. 3. Low Oxygen Tensions—Tests 2a, 2b, 2c (Homotypic grouping)

	(a) Brook	(b) Rainbow	(c) Brown
5 fish	18 gm.	20 gm.	18 gm.
Length of Exp.	142 min.	70 min.	53 min.
Temperature change	74°-73°	74°-74°	74°-74°
pH change	8.5-8.3	8.3-7.7	8.5-8.4
Free CO ₂	0-4.27	0-3.02	0-0
H. B. CO ₂	1.03-0	2.56-0	4.61-1.03
Fixed CO ₂	23.57-22.82	23.07-24.09	23.83-23.32
D. O.	3.76-1.98	3.64-2.31	3.76-2.99
Mortality (1st)	87 min.	27 min.	38 min.
Mortality (50%)	121 min.	48 min.	47 min.
Mortality (total)	142 min.	70 min.	53 min.
Average length of survival	118 min.	45.4 min.	46.8 min.

Dry ice (solid carbon dioxide) was used as a source of carbon dioxide. It was found that 1 gram of this substance placed in a gallon of creek water would raise the free carbon dioxide content to about 80 p.p.m. (40 cc./l.) and 2 grams to about 200 p.p.m. (100 cc./l.) In preparation for these tests two containers of equal volume were each given the same treatment. They were completely filled with water, and the same amount of dry ice was added to each. When it had ceased acting, they were stoppered so as to exclude air bubbles and inverted a few times to mix the contents. The trout were placed in one container and from the other, samples were taken for analysis. Because of the high CO₂ tensions it was difficult to handle such samples without having some of the gas escape. The results of a typical test are given in the table below.

Exp. 4. High CO₂ Tensions—Test 4 (Heterotypic grouping).

	150 min.	Brook	Rainbow	Brown
3 fish		13.0 gm.	13.5 gm.	13.0 gm.
Length of Exp.	Start Finish			
Temperature change	66°-69°			
pH change	5.0-5.1			
Free CO ₂	472.5-468.5*			
H. B. & F. CO ₂	9.74-12.3			
D. O.	8.92-6.17			
Mortality (1st)	80 min.	47 min.	36 min.	
Mortality (50%)	90 min.	58 min.	43 min.	
Mortality (total)	150 min.	113 min.	50 min.	
Average length of survival	106.7 min.	72.7 min.	43 min.	

* The loss in CO₂ probably occurred during the titration of the sample.

To determine the reaction to high alkalinity and acidity trout fingerlings were placed in NaOH and HCl solutions of various normalities. The pH of these solutions was not determined colorimetrically because of the lack of the proper indicator for these extreme ranges. A typical test for each condition is included.

Exp. 5. High Alkalinity (N 1000 NaOH)—Tests 5a, 5b, 5c, (Homotypic grouping)

	(a) Brook	(b) Rainbow	(c) Brown
5 fish	24.5 gm.	25 gm.	24 gm.
Length of Exp.	30 min.	30 min.	28 min.
Temperature change	69°-71°	69°-71°	69°-71°
H. B. CO ₂ (phenol. alk.) ¹	50.48-47.92	50.48-47.15	50.48-46.89
Fixed CO ₂ (M. O. alk.) ²	72.01-66.11	72.01-66.62	72.01-66.62
D. O.	9.75-8.21	9.75-8.39	9.75-8.58
Mortality (1st)	22 min.	21 min.	24 min.
Mortality (50%)	28 min.	24 min.	26 min.
Mortality (total)	30 min.	30 min.	28 min.
Average length of survival	27.2 min.	25 min.	26.4 min.

¹ Abbreviation for phenolphthalein alkalinity.

² Abbreviation for methyl orange alkalinity.

Exp. 6. High Acidity (N 1000 HCl)—Test 4 (Heterotypic grouping)

	Brook	Rainbow	Brown
Length of Exp.	65 min.		
3 fish	16.5 gm.	16 gm.	16 gm.
Start Finish			
Temperature change	68°-68°		
Free CO ₂ (Phenol. acid.)*	93.5-108.08		
D. O.	9.87-5.15		
Mortality (1st)	59 min.	43 min.	51 min.
Mortality (50%)	62 min.	44 min.	61 min.
Mortality (total)	65 min.	47 min.	62 min.
Average length of survival	62 min.	44.7 min.	58 min.

* Abbreviation for phenolphthalein acidity.

Experiment 7 was performed to determine the reaction of these "sensitive" fresh-water fish to strongly hypertonic salt solution. The following test will serve as an example.

Exp. 7. High Concentrations of NaCl (N 20)—Test 4 (Heterotypic grouping)

	Brook	Rainbow	Brown
Length of Exp.	127 min.		
3 fish	14 gm.	15 gm.	14 gm.
Start Finish			
Temperature change	68°-70°		
pH change	8.3-6.8		
H. B. & F. CO ₂	22.82-27.68		
D. O.	8.97-1.85		
Mortality (1st)	85 min.	85 min.	101 min.
Mortality (50%)	112 min.	123 min.	105 min.
Mortality (total)	127 min.	125 min.	115 min.
Average length of survival	108 min.	111 min.	107 min.

The most important data from thirty-six tests under these seven different conditions are assembled to form the tables presented in the description of experimental results.

Results

In experiment 1, fish were subjected to the accumulation of unfavorable conditions including the increase of temperature and carbon dioxide tension, and the decrease of dissolved oxygen and pH. The type of container used, whether an open-topped jar or a sealed bottle, did not appear to influence the results, although the fish were probably at a greater disadvantage physiologically in the open-topped vessel. From this group of tests it was determined that the lethal concentration of oxygen was less than 4 p.p.m. and that of carbon dioxide greater than 20 p.p.m. In none of these tests did the temperature exceed 75°, so it is not considered as a factor contributing to death in this case. In all succeeding experiments, in which the influence of a single factor was being tested, all other conditions were kept well above the lethal limits indicated in Exp. 1. In this way the mortality could be attributed, primarily at least, to the lethal factor which was introduced.

In most of the experiments, tests were made with the species in separate containers and also with the three in the same vessel. The relative length or order of survival was the same under both conditions.

TABLE 1.—Exp. 1. Straight Survival. 88 fish—4 tests.

Test	(a) Brook			(b) Rainbow			(c) Brown		
	Free CO ₂ p.p.m.	D. O. p.p.m.	Av. Length of Survival (min.)	Free CO ₂ p.p.m.	D. O. p.p.m.	Av. Length of Survival (min.)	Free CO ₂ p.p.m.	D. O. p.p.m.	Av. Length of Survival (min.)
1 a	24.63	2.38	138						
1 b				25.64	2.57	97			
1 c							23.63	3.55	135
2			126			96			81
3			239			111			97
4			136			102			97
Comparative value			160			102			103

In view of the results obtained in these tests, death resulted primarily from lack of oxygen. There was an increase in carbon dioxide content, but in no test did it approach the lethal point as determined in experiment 4. The relative acidity and temperature increased to some extent but did not exceed that found in the natural habitat of these fish.

The first brook trout was asphyxiated when the dissolved oxygen reached 2.38 p.p.m. (1.67 cc./l.) at a temperature of 71° F. The rainbow succumbed at a slightly higher oxygen content, 2.57 p.p.m. (1.8 cc./l.) at 74°, and the brown at a still higher content, 3.55 p.p.m. (2.49 cc./l.) at 74°.

The minimum oxygen requirements for these trout are not well known. Paton (1902) found that fatal conditions for young rainbow developed if the dissolved oxygen was reduced to 2 cc./l. (2.9 p.p.m.) or lower. Gardner and King (1922) give the asphyxial point for brown trout as from 0.8 cc./l. (1.14 p.p.m.) at 6.5° C. to 2.4 cc./l. (3.4 p.p.m.) at 25° C. Gutsell (1929) found that for a short time brook trout could endure oxygen content as low as 1.2 p.p.m., while with 2.3-2.5 p.p.m. rainbow and brown trout were asphyxiated in greater or less proportion.

Although not in accordance with the results obtained in this investigation, the common belief is that the brook trout has a higher oxygen requirement than other trout and that it can survive only in well aerated water.

REACTION TO HIGH TEMPERATURES

TABLE 2.—Exp. 2. High Temperatures. 91 fish—3 tests. Temperature given in degrees Fahrenheit.

Test	(a) Brook			(b) Rainbow			(c) Brown		
	Temp. 1st death	Temp. 50% mort.	Length of test (min.)	Temp. 1st death	Temp. 50% mort.	Length of test (min.)	Temp. 1st death	Temp. 50% mort.	Length of test (min.)
1	84°	85°	90	83°	85°	150	84°	85°	105
2	85°	85°	68	80°	85°	68	84°	85°	68
3	84°	86°	105	84°	86°	105	86°	86°	105
Av.	84°	85°		82°	85°		85°	85°	

Of the 91 fish killed in these tests only two, both of which were rainbow, died at temperatures below 84°, and those temperatures were 80° and 83°. Individuals of all three species began to show distress when the temperature exceeded the 80° mark. Between 84° and 86° death occurred very rapidly, and by the time 86° was reached, mortality was complete. This lethal point was quite uniform in all tests and was the same for all species and groupings.

Embody (1921) has obtained evidence of temperature tolerances which are very similar to those given above. Brook trout kept outdoors in wood troughs showed distress when the water temperature reached 83.3° F., and there was 20% mortality at 84.2°. The brown trout showed distress at 84.2°; 50% died at 85.5° and at 87° the mortality was 100%. The reaction of the steelhead (sea-run rainbow) was similar to that of the brown trout with distress at 84.2°, 24% mortality at 85.5° and total mortality at 87° F. According to Creaser (1930), these experiments by Embody are the only previous ones supporting the 80° F. endurance limit.

Most of the knowledge of temperature tolerance for these fishes has been obtained from field observations where temperature was probably not the only factor operating to cause death. Adams (1920) reports brown trout being killed when stream temperatures reached 84°. Embody (1921) found brook

trout in streams in New York where the temperature was 81° F. Brown trout were found in water as high as 83° F. and the steelhead at temperatures of 85° F. Powers (1929) found all streams of the Smokies above 18° without brook trout, those under 18° C. (65° F.) containing this fish. He does not believe summer temperatures above 19° C. for any period of time are tolerated by trout. F. W. King (1937) reports the finding of dead rainbow when water temperatures reached 84° F. Live fish were congregated near small spring inlets where the temperature was 10 degrees lower than the main stream. According to Needham (1938), rainbow are the most adaptable of trout and do well in warm or cold water, and can stand maximum summer temperatures up to 83° F., while the brown trout will survive in water up to 81° F. He believes the ideal summer temperature for brook trout to be around 66° F., but that they will survive slightly higher temperatures.

On the basis of field observations, temperatures from 68° to 70° have been proposed most often as the maximum for brook trout water. Experimental results have shown that much higher temperatures are necessary to cause death. It must be admitted that temperature may be a regulating factor in the distribution of the brook trout, but certainly brown and rainbow are not sharply limited by this factor, since they are often found in the lower portions of streams below the occurrence of brook trout. Temperature may be a limiting factor in itself and, in addition, indirectly by virtue of its influence on pH, carbon dioxide tension, the saturation point for oxygen, and food consumption.

Rising temperature diminishes the oxygen affinity of blood. On the basis of their investigations, Irving, Black, and Safford (1941) state that at low temperatures the brown trout has a loading tension greater than that of the brook and rainbow, whereas at high temperature the brook trout has the advantage of greater unloading tension. These specific differences would seem to indicate the possession of different types of hemoglobin, but on this point evidence is lacking.

Temperature seems to be important primarily as a result of the influence upon metabolic rate and the relative oxygen holding power of water, and probably becomes a limiting factor only when other conditions permit it to restrict the dissolved oxygen below the required minimum.

REACTION TO LOW OXYGEN TENSIONS

It was found that 20 brook trout lived, on the average, 118 minutes in water having a dissolved oxygen content of 3.76 p.p.m. (2.63 cc./l.) at the beginning of the test. Brown trout under similar conditions existed only for an average of 47 minutes. Twenty rainbow placed in water having a dissolved oxygen content of 3.64 p.p.m. (2.55 cc./l.) survived for an average time of 45 minutes. These results show a similarity in reaction of rainbow and brown trout to water of low oxygen content and the much longer survival of brook trout under quite the same conditions. As in the preceding experiment, the fish survived for fairly long periods of time under much more adverse conditions than they would ever encounter in their natural habitat.

The relative lengths of survival as shown in these tests can be interpreted

as indicating differences in rate of oxygen consumption. On this basis the rainbow and brown trout consume oxygen at a much higher rate than the brook and therefore, more rapidly deplete the oxygen supply to the lethal point. Little seems to be known of the actual rates of O_2 consumption of these fishes. The brook trout has been accredited with having a higher oxygen requirement than most fishes, which, it is suggested, is responsible for its selection of well aerated water of low temperature (Breder 1927, Creaser 1930).

In view of the high oxygen content found in all trout water surveyed and the great resistance shown in these tests, it would seem that the importance of oxygen may be somewhat overrated as a determining factor. Powers (1922) states that workers in fish respiration have found that fishes are able to survive at rather low oxygen tensions without any apparent ill effect.

TABLE 3.—Exp. 3. Low Oxygen Tensions. 54 fish—4 tests.

Test	(a) Brook			(b) Rainbow			(c) Brown		
	D. O. at finish p. p. m.	D. O. at finish p. p. m.	Avg. Length of Survival (min.)	D. O. at start p. p. m.	D. O. at start p. p. m.	Avg. Length of Survival (min.)	D. O. at start p. p. m.	D. O. at finish p. p. m.	Avg. Length of Survival (min.)
1	2.65	1.91	29	2.65	1.91	11	2.65	1.91	13
2	a 3.76	1.98	118	3.64	2.31	45	3.76	2.99	47
3	a 3.76	2.01	49	2.52	2.25	35	2.56	2.56	14
4	a 1.97	1.85	22	1.94	1.54	7	1.79	1.46	8
	b								
	c								
Comparative value			55			25			21

REACTION TO HIGH CARBON DIOXIDE TENSIONS

The lengths of survival of trout under the conditions of this experiment were very surprising. No reaction whatever was shown to concentrations of carbon dioxide of 200 p.p.m. or less. At higher concentrations the carbon dioxide seemed to act as an anaesthetic rather than as an active killing agent. When placed in solutions having a carbon dioxide content of 300-500 p.p.m., the fish soon turned on their sides in a stupified condition, but continued to show regular breathing movements for a considerable period of time.

As in previous experiments, the brook trout greatly exceeded the rainbow and brown trout in its resistance to high concentrations of carbon dioxide. Of the latter two species the rainbow showed the longer survival time in four out of six tests; however, the differences in time were not great, as the results show, and may not be significant.

In general, the action of carbon dioxide on fish, as in the case of other organisms, is that of a narcotic, stimulating in small quantities, intoxicating in larger quantities, and producing death in very large quantities (Shelford and

Allee 1913, and Wells 1913). It was evident that high concentrations of carbon dioxide markedly reduced the activity of trout. Since there is a direct relationship between activity and metabolic rate, it follows that the relatively long periods of survival under these conditions of high carbon dioxide may have been partially due to decreased oxygen consumption.

TABLE 4.—Exp. 4. High Carbon Dioxide Tension. 54 fish—6 tests.

Test	Free CO ₂ p.p.m.		D. O. p.p.m.		Av. Length of Survival (min.)		
	Start	Finish	Start	Finish	Brook	Rainbow	Brown
1	78.92	84.96	7.73	2.16	117	81	84
2	208.03	*164.63	7.19	2.6	102	73	80
3	348.47	*279.25	8.21	4.94	137	81	71
4	472.5	*468.5	8.92	6.17	107	73	43
5	502.7	575.2	8.39	7.65	44	21	17
6	576.6	592.2	8.36	7.73	30	13	11
Comparative value					90	57	51

* The decrease in CO₂ content is probably due to the escape of the gas when the water sample was taken.

TABLE 5.—Exp. 5. High Alkalinity (NaOH). 78 fish—6 tests.

		(a) Brook			(b) Rainbow			(c) Brown		
Test	N. of Sol.	D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)
		Start	Finish		Start	Finish		Start	Finish	
a 1 b c	N/2000	10.12	2.04	172	10.12	1.85	176	10.12	2.28	156
2	N/1500	9.13	2.81	71	9.13	2.8	83	9.13	2.8	59
a 3 b c	N/1500	9.32	4.81	94	9.32	4.81	75	9.32	6.36	70
4	N/1000	9.69	7.53	33	9.69	7.53	20	9.69	7.53	20
a 5 b c	N/1000	9.75	8.21	27	9.75	8.39	25	9.75	8.58	26
a 6 b c	N/1000	9.90	8.42	29	9.90	8.08	25	9.90	8.73	27
Comparative value				95				93		

Gutsell (1929) points out that trout are not susceptible to the effects of carbon dioxide. Of two brook trout and two rainbow trout, three survived for days in water containing 32 or 33 p.p.m. Powers (1934, 1937a, 1937b) reports cases of sudden epidemics of fish mortality in artificial ponds and natural waters, which were caused in several instances by a very small sudden rise (50-100%) in carbon dioxide tension, and gives an account of fish being killed by low carbon dioxide tension of the water or by free alkalinity (but not by the alkalinity or acidity of the water as such). He points out, however, that it is

generally high carbon dioxide tension that kills fish. Needham's observations (Needham 1938) have led him to the conclusion that carbon dioxide is not usually harmful unless accompanied by low oxygen supply.

REACTIONS TO HIGH ALKALINITY AND HIGH ACIDITY

This was one of the few groups of tests in which the brook trout showed no greater resistance than the rainbow and brown trout. The lengths of survival were approximately the same for all three species, although the brook trout did rank first in four of the six tests. In these tests the trout showed a tolerance of alkaline conditions which they would never encounter in their natural habitats. Concentrations of NaOH less than N/2000 produced no obvious effect, the trout finally dying from lack of oxygen. In transposing normalities to pH, it is found that alkalinity of pH 10.70 seemed to have no effect on the usual survival time, while at pH 10.82 the survival time for all three species was cut in half. The significance of these reactions will be considered in the discussion of the following experiment.

TABLE 6.—Exp. 6. High Acidity (HCl). 101 fish—9 tests.

		(a) Brook			(b) Rainbow			(c) Brown			
Test	N. of Sol.	D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)	
		Start	Finish		Start	Finish		Start	Finish		
a 1 b c	N/2000	9.07	3.33	183	9.07	6.05	82	9.07	5.18	148	
2	N/1000	9.5	6.17	49	9.5	6.17	37	9.5	6.17	53	
3	N/1000	9.35	5.8	52	9.35	5.8	39	9.35	5.8	54	
4	N/1000	9.87	5.15	62	9.87	5.15	45	9.87	5.15	58	
a 5 b c	N/1000	9.69	7.73	59	9.69	8.30	42	9.69	7.99	59	
6	N/500	8.89	7.00	20	8.89	7.00	16	8.89	7.00	26	
7	N/500	9.29	7.27	21	9.29	7.27	20	9.29	7.27	24	
8	N/500	8.82	7.21	26	8.82	7.21	20	8.82	7.21	30	
a 9 b c	N/500	9.57	8.03	34	9.57	8.21	25				
Comparative value				88				48			58

All three species lived for more than 2.5 hours in solutions of N/2000 HCl, and died only when the oxygen supply dropped below the minimum requirements. Higher concentrations brought to light species differences. The results show that the brook and brown trout have about the same degree of resistance to very acid conditions, whereas the rainbow is considerably less tolerant. If the solutions are considered in terms of approximate pH, then we see that at a pH of 3.3 (N/2000) the brook and brown trout seem to be little affected, while the rainbow showed a definite reduction of its survival time. At a pH of 3.0 (N/1000) all three species lived only 1/3 as long as they did in the solu-

tion of pH 3.3. These results, as far as the brook trout and rainbow are concerned, appear to verify the conclusions drawn from the field observations. The greater tolerance of the brook trout to acid conditions, as shown here, can be correlated with its occurrence in very acid streams from which the rainbow are absent.

Many investigations carried on to date have shown that aquatic organisms are able to withstand a wide range of pH. Of such studies on trout, the brook trout has received much greater attention, and the results obtained have been generalized, without sufficient evidence, to apply to other trout species. Coker (1925) suggested that the hydrogen-ion concentration seemed to be an important factor in determining the habitat of brook trout. He found pH readings in North Carolina and Massachusetts of 6.0 to 7.0. He called attention to the limited fish fauna of trout streams and suggested that trout inhabit neutral or acid water in contrast with most other fish. Davis (1926) recorded pH readings varying from 7.4 to 8.0 in Vermont trout streams, and believes that all streams in the vicinity are normally alkaline. The water of certain hatcheries which he tested varied in pH from 7.5 to 9.5. Breder (1927) states that the brook trout has a rather wide hydrogen-ion tolerance but is probably more tolerant of high acidity than of high alkalinity. Creaser and Brown (1927) found brook trout abundant in basic waters (pH 7.1-8.2) in northern Michigan and concluded that hydrogen-ion concentration has little to do with the tolerance of brook trout for a given habitat. Trout streams of the Ithaca region were found to be basic with a pH range of 7.6 to 8.4 (Gutsell 1929). Powers (1929) reports such extreme acidity as pH 4.1 in the brook trout streams of Tennessee. Pratt (1937) reports pH readings varying from 8.1 to 8.5 in the Gunnison River of Colorado, which is one of the great trout streams of America. These data give no indication that either acid or alkaline waters are more favorable or more generally preferred by brook trout.

TABLE 7.—Exp. 7. High Concentrations of NaCl. 42 fish—4 tests.

Test	N. of Sol.	(a) Brook			(b) Rainbow			(c) Brown		
		D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)	D. O. p.p.m.		Length Survival (min.)
		Start	Finish		Start	Finish		Start	Finish	
a	*N/500	9.01	2.13	155						
b					9.01	1.85	152			
c								9.01	2.22	157
2	*N/300	8.39	2.28	88	8.39	2.28	87	8.39	2.28	74
3	*N/50	9.22	1.79	114	9.22	1.79	113	9.22	1.79	97
4	*N/20	8.97	1.85	108	8.97	1.85	111	8.97	1.85	107
Comparative value				116				116		

* These normalities are the equivalent of the following percentages: N/500 = .12 0/00, N/300 = .20 0/00, N/50 = 1.20 0/00, N/20 = 2.90 0/00, N/5 = 11.7 0/00.

A test was run using N/5 NaCl, but at the end of an hour and a half the fish showed no distress, so the test was discontinued.

The direct effect on fish of hydrogen-ion concentration in itself may not be of great significance. The real importance of pH is its influence on the very vital process of respiration. An increase in hydrogen-ion concentration favors the dissociation of oxyhemoglobin; therefore, in an acid condition it cannot hold or transport as much oxygen as in a neutral condition. However, Creaser (1930) found that for brook trout hydrogen-ion concentrations throughout the range 4.1 to 9.5 did not seem to shift the voluntary toleration limits either of temperature or of dissolved oxygen content.

REACTION TO SODIUM CHLORIDE

In order to test the reaction of these fishes to a common salt, they were placed in various concentrations of sodium chloride. Solutions as concentrated as N/20 produced no deleterious effects. In such solutions the fish were able to reduce the oxygen content to a very low level before becoming asphyxiated. The results obtained in this group of tests have two main points of interest: first, that trout, which are considered very sensitive fishes, could exist for a considerable length of time in a hypertonic sodium chloride solution approximately one-tenth as strong as sea water (sea water is about N/2 or 3.5% NaCl); and second, the increased resistance shown by rainbow in these tests. Their survival times almost equalled and, in some cases, exceeded those of brook and brown trout. Very similar results were obtained when reactions to strongly alkaline solutions were being tested. Perhaps this can be related to certain migratory habits of the rainbow.

A summary of the results in the seven types of experimentation is presented in Table 8.

TABLE 8.—Summary of Results.

	No. of Tests	Brook		Rainbow		Brown	
		C. V. min.	Survival Longest in	C. V. min.	Longest Survival in	C. V. min.	Longest Survival in
1. Straight Survival	4	160	4 tests	102	0 tests	103	0 tests
2. High temperatures	4	Temp. of 1st death 84°	50% mort. at 85°	Temp. of 1st death 82°	50% mort. at 85°	Temp. of 1st death 85°	50% mort. at 85°
3. Low oxygen tension	4	55	4 tests	25	0 tests	21	0 tests
4. High CO ₂ tension	6	90	6 tests	57	0 tests	51	0 tests
5. High Alkalinity	6	95	4 tests	93	2 tests	83	0 tests
6. High Acidity	*9	88	2 tests	48	0 tests	58	6 tests
7. NaCl	4	116	2 tests	116	1 test	109	1 test

* In one test brook and brown had the same comparative value.

Discussion

It is known that "ecologically comparable animals living under similar conditions possess certain similarities of physiology, behavior, habits, and mode of life" (Shelford 1911). From this it is a logical deduction that animals occupying different habitats are doing so because of differences in their physiological make-up, behavior, habits, etc. It is to be expected that physical resistance or toleration is correlated with environment.

Surveys on numerous streams involving many miles of water revealed that brook and rainbow trout occupy different habitats with but a slight overlapping of ranges. The environment in which the brook trout is found is characterized by slightly higher oxygen content, lower carbon dioxide and lower temperature than the environment of the rainbow. Consequently, at the beginning of this study, it was anticipated that survival tests would show that the rainbow trout possesses a wider range of tolerance for the above named physical factors.

The results obtained in the experimental study, however, are to the contrary. They revealed degrees of tolerance much greater than trout are commonly believed to possess and that, of the three species tested, the brook trout is by far the hardiest fish. It exhibits markedly longer periods of survival under the majority of the experimental conditions. Thus, like many other investigators, we are led to the conclusion that the natural occurrence of a species cannot be explained entirely in terms of its reactions to environmental factors determined by laboratory experiment, that distribution is not a matter of tolerance alone.

The rôle of the physical environment in trout distribution cannot be completely disregarded as extremely high summer temperature is undoubtedly a limiting factor. A sufficiently low temperature has been considered the prime requisite of trout waters since trout culture began. Many investigators state definitely that temperature is the most important determining factor in trout distribution. Among the supporters of this idea are the following: Titcomb (1926), Kendall and Dence (1927), Gutsell (1929), Creaser (1930), Pratt (1937), and Needham (1938). Shelford and Allee (1913) state that the carbon dioxide content of the water is the best single index of its suitability for fishes. This may generally be true for warm-water fishes, but does not seem to apply to the specialized environment of trout. Powers (1929) seems to be of the opinion that temperature and carbon dioxide are both of great importance. W. King (1937) and the writer (King, J. 1937) have described observations which appear to show that hydrogen-ion concentration may be a limiting factor in certain localities.

It is well agreed that none of the species considered can survive for any length of time in water of much higher temperature than 80° F., but there is insufficient evidence indicating that the brook trout is less resistant to such conditions than the rainbow or brown trout.

There are other aspects of the problem which deserve consideration. It has been shown that there are considerable differences between the lethal limits

within which trout occur. Thus, it is seen that toleration, or reaction to natural conditions, and actual capacity for resistance, although interwoven, are still relatively independent. The response of fishes includes not only adjustments to the physical environment, but to biotic conditions as well. Fishes have definite habitat preferences which cause them to be definitely arranged in streams which have a graded series of conditions from mouth to source (Shelford 1911).

Any trout fisherman will agree that the rainbow is a more active fish than the brook trout. It rises to a fly quite differently and is thought to "put up more of a fight" when hooked. This difference showed up very strikingly when the fish were observed together during the experimental work. This greater activity, if it does actually exist, would indicate a higher metabolic rate. And, as is often the case, this difference in metabolic rate may be a cause or reflection of the greater susceptibility, as exhibited by the rainbow in the majority of the survival tests. Marsh (1908) reports some interesting observations on trout susceptibility to toxic substances in water which had remained in tin cans for some time. Water transported in new tinned fish cans was uniformly fatal to fry of the rainbow trout but had little effect on brook trout fry. This particular phenomenon is quite familiar to fish culturists and deserves further investigation. It is commonly recognized that brook trout can be transported in fish cans with more fish per can and less ice with lower mortality than is possible with rainbow.

Occasionally in the Smokies rainbow trout are taken which have reached a length of 24 to 26 inches. Brook are rarely seen exceeding the 16-18 inch size. It seems logical that the rainbow, being a relatively larger and possibly more active fish, would choose larger water, other conditions being the same, than the smaller and less active brook trout. Food supply and demand would also tend to restrict the larger fish to the bigger waters with their greater supply and variety of bottom organisms and minnows.

Few studies have been made on the compatibility of species, although such a factor is known to exist and to play a rôle in animal distribution. Kendall (1924) believes that real incompatibility may be indirect rather than direct. Thus, given three individuals of the same size, one of each species, it may be a question of which is the most "predaceous." He attributes the advantage on the part of the brown trout to the large size which it attains. Clemens (1917) states: "It has been proved conclusively that brown trout are very destructive to native brook trout. . . . Rainbow prefer larger bodies of water and show a tendency to work down from the upper streams into the lakes and larger streams. They are somewhat destructive to native trout and should not be planted in brook trout waters." Embury (1922) says, "It is believed that of the three trout the brown is the most predacious and most destructive of other fish, and it is often stated that if a stream is stocked with all three species, the brown trout will eventually exterminate the others." According to Pratt (1937), the headwaters of the Gunnison River in Colorado are inhabited by a native trout (*Trutta pleuriticus*) and eastern brook trout, while 15 miles down stream

the rainbow and brown trout form 90% of the trout population. He states, "In general, however, the trend in numbers of brown trout in relation to the number of rainbows has been gradually downward in the lower river." This suggests that the rainbow is at least on a par with the brown trout as far as aggressiveness is concerned. This aggressiveness may involve the matter of feeding habits and be more a competition for food than any actual antagonism of individuals, as indicated by W. King (1937).

Spawning requirements must also be considered a factor in the distribution of the species. The non-migratory habits of the brook trout would tend to restrict its range to those stream areas which satisfy its rather specific spawning requirements. On the other hand, the migratory rainbow could reside for the greater part of the year in the main body of the stream, where temperature and food supply are more favorable for rapid growth, and move into the headwater streams only for reproductive purposes.

It is recognized that conclusions based upon the results obtained in an investigation of this type must be drawn with reservations. The reactions of an animal are without doubt influenced by its physiological state at the time of the test. Individual variations may be caused by differences in size and age, degree of handling, time of last meal, etc. Careful technique can rule out many of these variables, but still the data secured apply only to that particular fish or group of fish under the specific conditions of the experiment.

The reactions of the hatchery-reared fish employed in these tests cannot be used in predicting the exact relations of wild trout in their natural habitat. Neither is it believed that a race of brook trout from Tennessee necessarily possess the same limitations as those of a race in a Vermont trout stream. However, it is assumed that there are physiological qualities common to the individuals of a species, and it is upon this hypothesis that the correlation of field and experimental data has been attempted.

It is concluded that the distribution of trout is not a matter of tolerance alone, since the limits of variability in natural waters are well within the extremes of the toleration range, but rather it is the result of the fishes' ability to choose their habitat through their reactions to both physical and biotic environmental factors. The latter seem to be of greater importance than is commonly realized. It is believed that each trout species, when unimpeded by topography, takes up a position in the stream suited to its "ecological constitution," a position where it fits harmoniously into the equilibrium of the organisms composing the animal and plant life of that body of water.

Summary

1. The reactions of brook, rainbow and brown trout fingerlings were tested under various experimental conditions: straight survival, high temperature, low oxygen tensions, high carbon dioxide tensions, high pH, low pH and high concentrations of NaCl.

2. As judged by length of survival under extreme conditions, the brook trout is the hardest fish of the three. All three species showed equal susceptibility to high temperature. The brook and brown trout were about equal in survival value in solutions of very low pH and greatly exceeded the rainbow in this respect. Under all other conditions the brook trout exhibited the greatest resistance in terms of longest survival.

3. Degrees of tolerance, not ordinarily believed possible, were found for these "sensitive" fish. The limits of variability of the natural habitat of each species are well within the extremes of the toleration range of all.

4. The distribution of trout is not a matter of toleration alone, but involves an actual choice of habitat. Each species takes up a position in the stream where the balance of biotic, as well as physical, conditions is compatible to its existence.

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New and Little Known Phalangids from the United States

Clarence J. Goodnight and Marie L. Goodnight

During the study of United States Phalangida in preparation for future monographing, several new species were encountered. Several other species whose relationships were not clear, were also studied and redescribed. Both the new and redescribed species are included in this paper with the hope that other workers will be able to understand better the relationships of the United States phalangid fauna.

The authors wish to thank Dr. W. J. Gertsch of The American Museum of Natural History for placing much of this material at their disposal and Dr. Nathan Banks of the Museum of Comparative Zoology for permitting them to examine certain types. They also wish to thank the collectors who contributed material. These collectors are listed after the described species.

Suborder LANIATORES Thorell

COSMETIDAE Simon

COSMETINAE Cambridge

Calicynorta, new genus

Cynorta (in part), Banks, 1893, Trans. Amer. Ent. Soc. 20:150; Banks, 1901, Amer. Natural. 35:671; Banks, 1904, Proc. Calif. Acad. Sci. (Ser. 3) 3:363; Banks, 1911, Pomona Journ. Ent. 3:415.

Eucynortella (In part) Roewer, 1912, Arch. Naturg. (10) 78A:53; Roewer, 1923, Die Weberknechte der Erde, p. 326.

Genotype.—*Calicynorta bimaculata* (Banks).

Diagnosis.—Dorsum with five areas, fourth area with median paired tubercles. Remaining dorsal areas and free tergites unbedecked. Tarsal segments 5—more than 6—6—6. Distitarsus of first tarsus with 3 segments, of second also 3. Basal segments of third and fourth legs not enlarged over those of the first and second.

A study of the holotype of *Cynorta bimaculata* Banks revealed that it was a member of a new genus closely related to *Kevonones* Chamberlin. *Calicynorta* differs from *Kevonones* by having tubercles on the fourth area of the dorsum.

Calicynorta bimaculata (Banks)

Fig. 1

Cynorta bimaculata Banks, 1893, Trans. Amer. Ent. Soc. 20:150; Banks, 1901, Amer. Natural. 35:671; Banks, 1904, Proc. Calif. Acad. Sci. (Ser. 3) 3:363; Banks, 1911, Pomona Journ. Ent. 3:415.

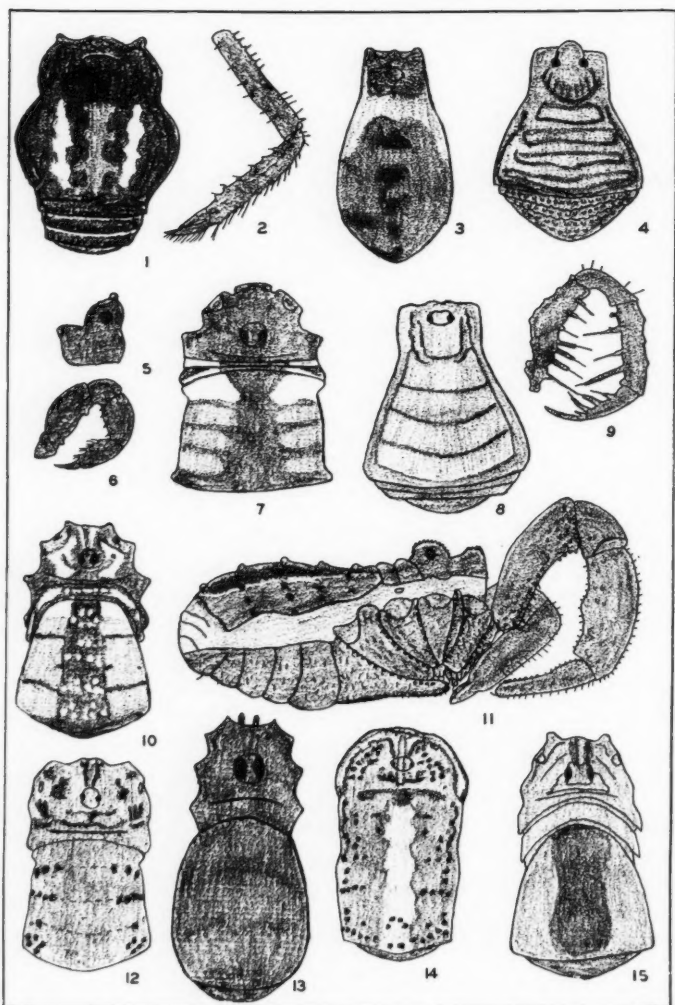


PLATE 1.—1, *Calicynorta bimaculata* (Banks), dorsal view of female. 2, *Taracus nigripes*, new species, retrolateral view of left chelicera of female. 3, *Idem*, dorsal view of female. 4, *Sclerobunus brunneus* Banks, dorsal view of male. 5, *Idem*, lateral view of eye tubercle of male. 6, *Idem*, retrolateral view of left palpus of male. 7, *Leiobunum bimaculatum* Banks, dorsal view of male. 8, *Sclerobunus cavicolens* (Banks), dorsal view

Eucynortella bimaculata Roewer, 1912, Arch. Naturg. (10) 78A:53; Roewer, 1923, Die Weberknechte der Erde, p. 326.

Holotype.—Female from San Diego, California. In the collection of the Museum of Comparative Zoology.

Description of holotype: Total length of body, 3.7 mm. Length of Cephalothorax, 1.0 mm. Width of body at widest portion, 3.0 mm. Dorsum finely granulate, with a row of small tubercles along the posterior margin of the fifth area and the free tergites. Eye tubercle low, normal; no median spines on the dorsum. A pair of tubercles on the fourth area. Venter and coxae finely granulate.

Legs: clothed only with a few scattered hairs and tubercles. Third and fourth legs not enlarged over the first and second. Tarsal segments 5-9-6-6. Distitarsus of first tarsus 3, of second 3.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.3	1.3	0.5	0.8	1.2	0.7	4.8 mm.
II	0.3	2.3	0.6	1.9	2.2	1.7	9.0 mm.
III	0.3	1.6	0.6	1.1	1.8	1.0	6.4 mm.
IV	0.4	2.3	0.7	1.5	2.3	1.1	8.3 mm.

Palpus: trochanter 0.2 mm. long, femur 0.7, patella 0.5, tibia 0.9, and tarsus 0.4. Total length, 2.7 mm. Palpus normal, characteristically flattened.

Chelicerae normal.

Dorsum reddish brown with lighter markings faintly outlining the areas. The median line lighter. On either side of the median line, midway between the median line and the lateral margin of the dorsum is a long narrow white spot extending from the first area through the fourth. Venter, chelicerae, and palpi reddish brown. Legs yellowish red, somewhat lighter.

TRIAENONYCHIDAE Soerensen

TRIAENONYCHINAE Pocock

SCLE ROBUNUS BRUNNEUS Banks

Figs. 4, 5, and 6

Sclerobunus brunneus Banks, 1893, Trans. Amer. Ent. Soc. 20:152; Banks, 1911, Pomona Journ. Ent. 3:416; Roewer, 1914, Arch. Naturg. 80A:88; Roewer, 1923, Die Weberknechte der Erde, p. 597.

Sclerobunus robustus, Roewer, 1931, Zeit. Wiss. Zool. 138:153.

Cotype.—Male from Olympia, Washington. Female from same locality. Both in the collection of the Museum of Comparative Zoology.

Description of cotype: Male, total length of body, 2.0 mm. Length of cephalothorax, 0.7 mm. Width of body at widest portion, 1.4 mm. Dorsum

of male. 9. Idem, retrolateral view of left palpus of male. 10. *Leiobunum trimaculatum*, new species, dorsal view of male. 11. *Protolophus rossi*, new species, lateral view of male. 12. *Eurybunus pallidus*, new species, dorsal view of male. 13. *Mesosoma texana*, new species, dorsal view of male. 14. *Eurybunus riversi*, new species, dorsal view of male. 15. *Leiobunum oregonense*, new species, dorsal view of male.

with five distinct areas which are parallel to one another. Entire dorsum faintly granulate with rows of larger granulations on the free tergites. First area of dorsum without a median line. Eye tubercle in the form of a rounded cone, located on the anterior margin of the cephalothorax. Venter and coxae granulate, lateral teeth present on the anterior and posterior margins of coxa III and on the posterior margin of coxa IV.

Legs: clothed with short scattered hairs and granulations. Legs relatively heavy. Astragalus of the metatarsi greater in length than the calcaneus. Tarsal segments 3-5-4-4. Distitarsus of tarsus of first leg with 2 segments, of second, with 3.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.2	0.5	0.3	0.4	0.4	0.4	2.2 mm.
II	0.2	1.0	0.4	0.8	0.9	0.7	4.0 mm.
III	0.2	0.5	0.3	0.5	0.6	0.5	2.6 mm.
IV	0.3	0.9	0.4	0.7	1.0	0.6	3.9 mm.

Palpus: trochanter 0.2 mm. long, femur 0.4, patella 0.3, tibia 0.4, and tarsus 0.4. Total length, 1.7 mm. Palpus as in Fig. 6. Entire dorsal surface granulate.

Chelicerae: proximal segment with a slight elevation on the dorsal surface. Second segment short, clothed with hairs.

Entire animal reddish brown with the areas and free tergites outlined in a darker color. Appendages concolorous.

Description of cotype: female, total length of body, 2.3 mm. Length of cephalothorax, 0.6 mm. Width of body at widest portion, 1.7 mm. Female identical in appearance with male; but lacking the raised area on the proximal segment of the chelicera.

Sclerobunus cavicolens (Banks)

Figs. 8 and 9

Cytobunus cavicolens Banks, 1905, Ent. News **16**:251, figs. 1 and 2; Roewer, 1915, Arch. Naturg. **80A**:62, fig. 12; Roewer, 1923, Die Weberknechte der Erde, p. 631. *Sclerobunus robustus*, Crosby and Bishop, 1924, Ent. News **35**:109; Roewer, 1931, Zeit. Wiss. Zool. **138**:153.

Holotype.—Immature specimens from Morrison's Cave, 60 miles West of Bozeman, Montana. Several males and females studied were from the type locality. These were collected February 22, 1941, by H. B. Mills and A. L. Jellison. These specimens were compared with the holotype which is in the collection of the Museum of Comparative Zoology.

Description of male: total length of body, 2.0 mm. Length of cephalothorax, 0.7 mm. Width of body at widest portion, 1.6 mm. Dorsum finely granulate, abdominal scute with five distinct areas, the boundaries of which are parallel to one another. First area without a median line. All dorsal areas and free tergites unbedecked. Eye tubercle in the form of a low rounded eleva-

tion, clearly removed from the anterior margin of the cephalothorax. Venter granulate, spiracle not visible. Coxae I to III have a few spine-like hairs. All coxae with small tubercles at the distal ventral margin.

Legs: clothed only with scattered hairs except for leg I. The trochanter of leg I has one spine-bearing tubercle, and the femur has two. The second leg has an extremely long first tarsal segment, other legs have first tarsal segment longer than the remaining ones. Astragulus of the metatarsi much longer than the calcaneus. Lateral projections of the third and fourth claw very small, barely discernible. Tarsal segments 3-5-4-4. Distitarsus of first tarsus with 2 segments, of second with 3.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.2	0.9	0.4	0.7	1.0	0.7	3.9 mm.
II	0.2	1.5	0.5	1.6	1.6	1.7	7.1 mm.
III	0.3	1.2	0.4	1.0	1.5	1.4	5.8 mm.
IV	0.3	1.4	0.4	1.3	1.9	1.1	6.4 mm.

Palpus: trochanter 0.2 mm. long, femur 0.7, patella 0.4, tibia 0.7, and tarsus 0.6. Total length 2.6 mm. Palpus armed as in Fig. 9. In addition on the prolateral margin of the femur two spine-bearing tubercles on the apical median portion. The extreme apical tubercle is sometimes very reduced. One spine-bearing tubercle on the prolateral margin of the patella. Tibia and tarsus armed as on the retrolateral side.

Chelicerae: normal, clothed with a few small hairs and tubercles.

Entire dorsum light yellow, with a slightly darker mottling on the lateral portion of the cephalothorax and the anterior part of the abdomen. Eyes black, strongly contrasting with the light tubercle. Venter and appendages concolorous with the dorsum.

Description of female: total length of body, 2.1 mm. Length of cephalothorax, 0.6 mm. Width of body at widest portion, 1.8 mm. Similar in appearance to male except that the spines of the femur of the first leg are somewhat reduced.

Sclerobunus cavicolens (Banks) was originally described in the genus *Cyrtobunus*; however examination of the holotype and numerous specimens from the type locality revealed that they belonged to *Sclerobunus*. *S. cavicolens* is a valid species and not a synonym of *Sclerobunus robustus* Packard.

Suborder PALPATORES Thorell

Tribe DYSPOI Hansen and Soerensen

ISCHROPSALIDAE Simon

Taracus nigripes, new species

Fig. 2 and 3

Holotype.—Female, from Wolf Creek Pass, elevation 10,000 ft., Colorado, July 22, 1941. Female paratypes from same locality. C. J. and M. L. Good-

night collectors. All in the collection of The American Museum of Natural History.

Description of holotype: length of body, 3.6 mm. Length of cephalothorax, 0.9 mm. Width of body at widest portion, 2.3 mm. Dorsum smooth, covered with widely separated, extremely small black spines. Cephalothorax arched. Eye tubercle smooth, not canaliculate. Cephalothorax and first abdominal segment lacking the small black spines. Posterior to the eye tubercle a small forward pointing spine, characteristic of the genus. Free sternites with numerous small black spines. These black spines become longer and more numerous on the genital operculum and coxae. Coxae without lateral teeth.

Legs: armed with scattered black spines which are more numerous on the basal segments. Metatarsi with false articulations.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.3	1.4	0.4	1.2	1.4	1.0	5.7 mm.
II	0.3	2.0	0.4	1.5	2.3	2.2	8.7 mm.
III	0.3	1.4	0.5	1.0	1.4	1.2	5.8 mm.
IV	0.3	1.8	0.6	1.7	2.1	1.5	8.0 mm.

Palpus: trochanter 0.3 mm. long, femur 1.7, patella 1.1, tibia 0.9, and tarsus 0.3. Total length, 4.3 mm. Palpus slender as is characteristic of the genus. Trochanter, femur, and patella armed with scattered black spines. Tibia and tarsus thickly covered with light spinose hairs. Tarsus very small, folded back against the tibia.

Chelicerae: long, proximal segment 1.6 mm. long. Distal segment 1.4 mm. long. Proximal segment armed with scattered spine-bearing tubercles. Distal segment likewise armed with numerous spine bearing tubercles. These tubercles more or less arranged in several rows giving an angular appearance. Cheliceral jaws armed distally with small inner teeth.

Cephalothorax and eye tubercle very dark brown with a few darker brown markings laterad to the eye tubercle. Small spine posterior to the eye tubercle dark brown. First abdominal segment and the small lateral portion of the cephalothorax adjoining it silvery white. Remaining abdominal segments silvery with a brownish overcast. In the median posterior portion of each segment is a brown spot. The small spines covering the abdomen are black, but so small as to be scarcely discernible. Each spine arising from a small darker brown dot. Free sternites and genital operculum silvery with black spines. Spiracle dark brown, contrasting vividly. Coxae brownish with dark spines. Trochanters brown, a lighter brown portion present at the base of each femur. Femur, patella, and tibia of legs dark brown, metatarsi and tarsi lighter brown. Spines on legs black. Palpi very dark brown, almost black except for a lighter portion at the base of the femur. Entire chelicera deep black.

T. nigripes shows affinities to *T. packardi* Simon, but differs by having dark colored legs and palpi.

Tribe EUPNOI Hansen and Soerensen

PHALANGIIDAE Simon

LEIOBUNINAE Banks

LEIOBUNUM BIMACULATUM Banks

Fig. 7

Leiobunum bimaculatum Banks, 1893, *Canad. Ent.* 25:210; Banks, 1901, *Amer. Nat.* 35:676; 1904, *Banks, Proc. Calif. Acad. Sci.* 3:361; Roewer, 1910, *Abh. Ver. Hamburg* 19(4): 229; Banks, 1911, *Pomoma Journ. Ent.* 3:421; Roewer, 1923, *Die Weberknechte der Erde*, p. 905.

Holotype.—Male from southern California. In the collection of the Museum of Comparative Zoology.

Description of holotype: total length of body, 4.1 mm. Length of cephalothorax, 1.7 mm. Width of body at widest portion, 3.3 mm. Dorsum granulate, truncate caudad as seen from above. Eye tubercle not canaliculate, with several small spinules over each carina. Venter and coxae granulate, lateral teeth present on the anterior margin of all coxae and on the posterior margin of coxa IV.

Legs: long and slender. Femur I, 13 mm. long; femur II, 21 mm.; femur III, 12 mm.; and femur IV, 16 mm.

Palpus: femur not extending above the dorsum. Femur armed ventrally with small tubercles and hairs. Tibia likewise armed. Patella and tarsus clothed with hairs. Tarsal claw small and black, toothed.

Chelicerae normal.

Dorsum dark chocolate brown, eye tubercle concolorous, slightly lighter on the interior basal portion. A large white spot at the junction of the abdomen and the cephalothorax, broken into three spots by the folds separating the cephalothorax from the abdomen. Venter and coxae ash-grey. Trochanters yellowish brown, not contrasting very strongly with the coxae. Legs yellowish brown. Palpi and chelicerae concolorous with the legs.

Leiobunum oregonense, new species

Fig. 15

Holotype.—Male from Rain Rock, Lane County, Oregon. Collected by Borys Malkin. Holotype in the collection of The American Museum of Natural History. Male and female paratypes from Car Canyon, California. Collected August 9, 1940, by E. S. Ross. In the collection of the California Academy of Sciences.

Description of holotype: total length of body 5.5 mm. Length of cephalothorax, 1.4 mm. Width of body at widest portion, 3.6 mm. Dorsum coarsely granulate. Eye tubercle canaliculate, smooth above, situated on the median portion of the cephalothorax, constricted at the base. Abdomen subtruncate as seen from above. Supra-cheliceral lamella extended into two blunt spines. Venter and coxae granulate, genital operculum with lateral rows of teeth. On the anterior and posterior margins of coxae I to IV small teeth present. In the holotype these teeth are so reduced as to be scarcely discernible. These teeth are quite large in the specimens from California. Penis elate.

Legs: armed with small black spines more or less arranged in rows on all segments but the metatarsi and tarsi. Metatarsi with numerous false articulations. Femur I, 8 mm. long; femur II, 13 mm.; femur III, 8 mm.; and femur IV, 11 mm.

Palpus: trachanter 0.4 mm. long, femur 1.4, patella 0.7, tibia 0.9, and tarsus 1.4. Total length, 4.8 mm. Palpus armed throughout with numerous black spines. Tarsal claw toothed. Femur not extending above the eye tubercle.

Chelicerae normal.

Dorsum golden with a faint suggestion of a median darker stripe. A few lighter punctate dots present at the junction of the abdominal segments. Eye tubercle yellowish, eyes black. A few darker brown markings present in the region from the eye tubercle to the anterior margin of the cephalothorax. Venter and coxae yellowish, lateral teeth brown. Trochanters light with a few darker mottlings, not contrasting with the coxae. Legs brownish, darker distally. Palpus yellowish brown with some darker brown present at the apical portion of the femur, and some mottlings on the patella and tibia. Chelicerae concolorous with the dorsum.

Description of paratype: female, total length of body, 3.8 mm. Length of cephalothorax, 1.3 mm. Width of body at the widest portion, 2.8 mm. Identical in appearance with the male.

This species differs from the other western *Leiobunum* in the appearance of the dorsum.

Leiobunum trimaculatum, new species

Fig. 10

Leiobunum bimaculatum, Crosby and Bishop, 1924, Journ. Elisha Mitchell Sci. Soc. 40:13-16, pl. 2, figs. 11 and 12; Davis, 1934, Amer. Midl. Nat. 15:669, pl. 31, fig. 8.

Holotype.—Male holotype and male and female paratypes from Ocala, Florida. Collected September 1 1940, by C. J. and M. L. Goodnight. All specimens in the collection of The American Museum of Natural History.

Description of holotype: length of body, 3.1 mm. Length of cephalothorax, 1.4 mm. Width of body at widest portion, 2.5 mm. Dorsum finely granulate, eye tubercle high, not canaliculate, constricted at the base, located at the posterior portion of the cephalothorax. A few very small tubercles over each carina. Venter and coxae with numerous small tubercles and a few scattered hairs. Lateral teeth present on the anterior margins of coxae I to IV and on the posterior margin of coxa IV.

Legs: clothed only with a few small scattered hairs, a few small black spines on the basal segments. Femur I, 14 mm. long; femur II, 18 mm.; femur III, 13 mm.; femur IV, 18 mm.

Palpus: trochanter 0.4 mm. long, femur 1.1, patella 0.5, tibia 0.7, and tarsus 1.3. Total length, 4.0 mm. Clothed with scattered hairs. Femur not elevated above the eye tubercle. Palpal claw toothed.

Chelicerae normal.

Dorsum brownish, eye tubercle concolorous, lighter at the anterior basal portion. A series of light spots at the lateral portion of each abdominal segment, giving the appearance of a darker dorsal stripe on the median line. The first two spots are much lighter, being silvery in color. The lateral portion of the cephalothorax bears irregular lighter markings. Two small lighter stripes pass from the eye tubercle to the anterior margin. There are a few small lighter punctations on each abdominal segment within the darker median stripe. Venter and coxae light yellowish, trochanters concolorous, legs yellowish brown, darker distally. Chelicerae and palpi concolorous with the venter.

In the more northern specimens, those from the Carolinas, etc., the dorsum is extremely dark, almost black. Eye tubercle black. The two anterior spots on the abdomen stand out strongly as yellow against the dark background. The yellowish markings of the lateral portions of the cephalothorax are reduced to a small white marking at the posterior margin. Otherwise these specimens are identical with the more southern forms. Specimens from most of the southeastern states were studied.

Description of female: total length of body, 4.9 mm. Length of cephalothorax, 1.4 mm. Width of body at widest portion, 3.1 mm. Identical in appearance with male.

In previous literature, this species has been referred to as *L. bimaculatum* Banks, following Crosby and Bishop's interpretation (1924). An examination of the holotype of *L. bimaculatum* Banks reveals that it has a somewhat different arrangement of these spots. When *L. bimaculatum* and *L. trimaculatum* are seen side by side, they are quite distinct.

Mesosoma roeweri, new species

Phalangium nigrum Wood, 1870, Comm. Essex Inst. 6:34-35;

Astrobus nigrum, Weed, 1890, Amer. Nat. 24:683.

Mesosoma nigrum, Weed, 1893, Trans. Amer. Ent. Soc. 20:286, Roewer, 1910, Abh. Ver. Hamburg 49:258; Roewer, 1923, Die Weberknechte der Erde, p. 920.

Holotype.—Male from Houston, Texas. Collected June 11, 1937, by S. Mulaik. Holotype in the collection of The American Museum of Natural History.

A new species is proposed for the *Mesosoma* described by Roewer in "Die Weberknechte der Erde," p. 920 as *M. nigrum*. The true *M. nigrum* described by Say from the southeastern portion of the United States differs from *roeweri* by having small three-pronged lateral coxal teeth. *M. roeweri* has conspicuous blunt teeth, and also has the ventral portion of the femur of the palpus armed with spines rather than with hairs as in *nigrum*. A specimen of the true *nigrum* from Illinois has been incorrectly referred to as *M. ephippiatum* in "Die Weberknechte der Erde." Thus Roewer's *M. ephippiatum* becomes a synonym of *M. nigrum* Say.

Records: Liberty, Texas, June 12, 1937; Orange, Texas, June 12, 1937,

and Jasper, Texas, June 6, 1940. All collected by S. Mulaik. Further records from Corpus Christi, Texas, July 15, 1935, collector, H. C. Sibley, Jr., and from Austin, Texas, September, 1909, collector, A. Petrunkevitch.

Mesosoma texanum, new species

Fig. 13

Holotype.—Male from Goose Creek, Texas, October, 1931. Holotype in the collection of The American Museum of Natural History.

Description of holotype: total length of body, 5.3 mm. Length of cephalothorax, 1.5 mm. Width of body at widest portion, 3.6 mm. Dorsum coarsely granulate, giving a pebble-like appearance. Eye tubercle in the median portion of the cephalothorax, wider than high, covered with coarse granulations. Abdominal segments united closely in a hard dorsal scute, characteristic of the genus. A very small elevation at the median anterior margin of the cephalothorax. Supra-chelicerar lamella prolonged into two obtuse spines. Venter and coxae with scattered granulations. Lateral teeth present on the margin of the genital operculum and on the fore and hind margins of coxae I to IV. Coxal teeth very much reduced on the posterior margin of coxa III. These coxal teeth are bluntly rounded blocks, somewhat similar to those of *M. roeweri*, but slightly more rounded.

Legs: armed with small scattered spines on all segments but the metatarsi and tarsi. Metatarsi with false articulations.

Palpus: trochater 0.3 mm. long, femur, 0.8, patella, 0.3, tibia 0.6, and tarsus, 1.1. Total length, 3.1 mm. Palpus armed with scattered hairs. A few small spines on the ventral portion of the tibia. Ventral portion of the femur clothed only with hairs, not with the spines and tubercles as in *M. roeweri*. Tarsal claw with very small teeth.

Chelicerae normal.

Entire dorsum including the eye tubercle black. Free sternites reddish brown shading into darker brown at the lateral portions. Genital operculum and coxae reddish brown. Lateral teeth brown. Trochanters and proximal portion of the femora reddish brown, shading distally into black. Distal half of femur, patella, and tibia black. Proximal portion of metatarsi dark, shading into reddish brown at the distal portion. Tarsus reddish brown. Trochanter of palpus dark reddish brown, femur, patella, and tibia black. Tibia lighter ventrally, tarsi light brown.

M. texanum shows its closest affinities to *M. roeweri*, differing mainly in the darker color of the dorsum.

LEPTOBUNINAE Banks

Protolophus rossi, new species

Fig. 11

Holotype.—Male from Moticeto, California. In the collection of the Cali-

fornia Academy of Science. Female allotype from same locality. In the collection of The American Museum of American History. Both collected, February 22, 1938, by E. S. Ross.

Description of holotype: total length of body, 5.9 mm. Length of cephalothorax, 2.1 mm. Width of body at widest portion, 3.6 mm. Dorsum finely granulate, the five pairs of median elevations characteristic of the genus are very low in this species. The fifth pair being so low as to be discernible with difficulty. These tubercles are unspined, although a few have some very short hairs. Eye tubercle low, not canaliculate, armed with a row of tubercles over each eye. Median anterior margin of the cephalothorax characteristically elevated. This elevation armed with small black tubercles more or less arranged in four rows. Supra-chelicerar lamella with a pair of small blunt spines. Posterior part of the cephalothorax with a few very small scattered black spines. Free sternites and genital operculum armed with scattered black spines, the lateral margin of the genital operculum with a row of teeth. Second maxillar lobes straight and armed with black spines. Coxae with scattered black spines, lateral teth present on the anterior margins of coxae I to IV and on the posterior margins of coxae I and IV.

Legs: armed throughout with scattered black spines. Metatarsi without false articulations.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.4	1.9	0.7	2.1	2.2	3.4	10.7 mm.
II	0.5	2.7	0.9	2.9	2.7	6.8	16.5 mm.
III	0.5	2.0	0.7	2.0	2.5	4.0	11.7 mm.
IV	0.5	3.0	1.1	2.7	3.8	4.7	15.8 mm.

Palpus: trochanter 0.4 mm. long, femur 2.7, patella 0.8, tibia 2.1, tarsus 1.8. Total length 7.8 mm. Palpus large, armed throughout with scattered black spines. Ventrally armed with heavy tubercles. At the distal portion of the tarsus these ventral tubercles are very thick and heavy. Tarsal claw small, untoothed. Palpus strongly curved, this curving due to a curve at the distal portion of the femur and in the tibia. These two curves giving a bow-like appearance to the palpus. Femur 1.0 mm. wide.

Chelicerae large, normal. Armed dorsally with scattered hairs.

Dorsum yellowish brown with a darker brown median stripe, This darker brown encloses most of the cephalothorax, narrows to a stripe on the abdomen, just enclosing the tubercles. This stripe ends at the posterior margin of the fifth dorsal segment. Darker brown punctate markings mark the junctions between the abdominal segments. The lateral margins of the cephalothorax and abdomen and posterior portion of the abdomen, lighter, almost white. Eye tubercle darker at base, lighter above. Free sternites, coxae, and genital operculum silvery, the black spines contrasting strongly. Trochanters light, remainder of legs somewhat darker with dark brown mottlings. Metatarsi lighter than the remainder of the legs. Palpus brownish except for the tarsus which is quite light. Spines on palpus black. Chelicerae very light except for some brown markings on the proximal segment and the tips of the jaws which are black.

Description of allotype: total length of body, 5.2 mm. Length of cephalothorax, 1.4 mm. Width of body at widest portion, 3.2 mm. Female similar in appearance to the male except that the palpi are not enlarged. The characteristic apical median patellar spur is present. Dorsal tubercles barely discernible.

P. rossi shows its closest affinities to *P. singularis* Banks. It differs markedly, however, in the dorsal color pattern, the shape of the palpus, and in the heavy tuberculation of the palpus.

PHALANGIINAE Simon

Eurybunus pallidus, new species

Fig. 12

Holotype.—Male, from Scottsdale, Arizona. Female allotype from same locality. Both collected by H. Britcher. In the collection of The American Museum of Natural History.

Description of holotype: total length of body, 3.3 mm. Length of cephalothorax, 1.4 mm. Width of body at widest portion, 2.5 mm. Dorsum smooth, eye tubercle normal, scarcely canaliculate, low, smooth above. The median anterior portion of the cephalothorax is elevated and notched slightly as is characteristic of the genus. This elevation extends posteriorly almost to the eye tubercle. It is roughly triangular in shape. The anterior portion of this elevation is set with numerous small black spines. Supra-cheliceral lamella smooth. Free sternites smooth, a few small black spines present on the genital operculum, maxillary lobes and coxae. Second maxillary lobes curved. Coxae without lateral teeth, a spine present at the anterior distal portion of the fourth coxae.

Legs: armed with a few scattered black spines more or less definitely arranged in rows on the femora of the second and fourth legs. Spines much more numerous on the ventral surface than on the dorsal surface of the tibiae and metatarsi. First and third legs with femur, patella, and tibia enlarged as is characteristic of the genus. Metatarsus of the second leg with two false articulations, of the fourth, one. Tibia of the second leg with three false articulations.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.4	1.5	0.4	1.6	1.9	2.7	8.5 mm.
II	0.4	3.2	1.1	3.2	2.7	5.4	16.0 mm.
III	0.4	1.4	0.7	1.4	2.2	3.2	9.3 mm.
IV	0.4	2.3	0.9	1.8	3.2	4.5	13.1 mm.

Palpus: trochanter 0.2 mm. long, femur 0.8, patella 0.4, tibia 0.4, and tarsus 0.9. Total length 2.7 mm. Palpus normal, armed throughout with small scattered black spines. Tarsal claw simple. Scattered spines most numerous on the tarsus.

Chelicerae normal, proximal segment without a ventral tooth, but with a slight elevation at the apical median portion. Slight elevation of the second segment also present.

Dorsum yellowish brown, silvery in some specimens. Eye tubercle also

yellowish brown. Dorsum with darker brown mottlings. The brown mottlings are especially numerous on the lateral and posterior portions of the cephalothorax. The median elevation has two long and two short brown stripes. On the lateral portion of the boundaries of the abdominal segments there are several brown spots. Towards the posterior portion of the abdomen, these become less regularly arranged. Venter and coxae silvery, legs light yellowish brown with a few brown spots on the femur, patella, and tibia. Palpi and chelicerae yellowish brown with a few darker mottlings.

Description of allotype: total length of body, 3.1 mm. Length of cephalothorax, 1.2 mm. Width of body at widest portion, 2.0 mm. Similar in appearance to male except that it lacks the secondary sexual characters, i.e., raised portions of the chelicerae.

This species differs from *E. brunneus* in being smaller and in having a lighter coloration. It differs from *E. spinosus* by lacking the spines of the dorsum.

***Eurybunus riversi*, new species**

Fig. 14

Holotype.—Male from Reno, Nevada. Collected April 19, 1941, by Ira LaRivers. Male paratype from Montgomery Canyon, Mono County, California. Collected July 13, 1941, by W. M. Pearce. Both in the collection of The American Museum of Natural History.

Description of holotype: total length of body, 5.4 mm. Length of cephalothorax, 2.1 mm. Width of body at widest portion, 2.9 mm. Dorsum finely granulate, eye tubercle low, not canaliculate, smooth above. Median anterior portion of the cephalothorax with the characteristic notched elevation. This elevation is covered with small black spines. From the margin it slopes posteriorly ending just anterior to the eye tubercle, roughly in the form of a triangle. Posterior part of the abdomen distinctly truncate as seen from above. Free sternites smooth, a few scattered black spines on the genital operculum. Second maxillary lobes slanted anteriorly and armed with scattered black spines. Coxae with a few scattered black spines. First to third coxae with small black tubercles which on coxa I become extremely numerous. Supra-cheliceral lamella smooth.

Legs: trochanters with a few scattered black spines and with small black tubercles on trochanter I to III. Femur, patella, and tibia of first and third legs characteristically enlarged. All segments of all legs armed with scattered black spines, the spines being especially numerous and large on the ventral portion of the first and third legs. The metatarsi of the first and third legs armed ventrally with two rows of sharp black spines. Two false articulations in the metatarsus of the second leg, one in the metatarsus of the fourth. Tibia of second leg with three false articulations.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	0.4	1.6	0.9	1.8	2.3	2.9	9.9 mm.
II	0.5	5.1	1.0	4.8	3.2	4.5	19.1 mm.
III	0.5	1.8	0.7	1.8	3.1	2.9	10.8 mm.
IV	0.5	3.6	1.0	2.9	4.1	4.9	17.0 mm.

Palpus: trochanter 0.3 mm., femur 0.7, patella 0.5, tibia 0.6, and tarsus 0.9. Total length, 3.0 mm. Palpus armed throughout with small black spines which are very numerous on the tibia and tarsus. Ventrally there are some heavier black spines on the trochanter, femur, and tibia. Tarsal claw untoothed.

Chelicerae normal. Armed with scattered black spines.

Dorsum dark brown with a suggestion of an irregular lighter median stripe. Lighter area in the anterior median portion of the cephalothorax. A lighter area also along the lateral margin of the cephalothorax and the anterior abdominal segments. Eye tubercle brownish. There are also some dark brown markings irregularly arranged on either side of the cephalothorax. On the abdomen these dark markings are in the form of round spots roughly following the divisions of the abdominal segments, becoming more regular at the posterior portion. Except at the posterior portion, they are lacking in the median lighter marking. Venter and coxae lighter, yellowish brown. The dark armature of the coxae contrasting strongly. Trochanters concolorous with the coxae. Femur, patella, and tibia of first and third legs and distal portion of the femur, patella, and tibia of the second and fourth legs dark brown. Remainder of legs yellowish brown. Chelicerae and palpi yellowish brown, the black spines contrasting strongly.

The paratype from California has longer legs than the holotype. Also the tubercles on the first and second coxae are light brown instead of black.

E. riversi differs from other species of *Eurybunus* mainly in its distinct dorsal color pattern.

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Records and Descriptions of North American Plecoptera

Part III. Notes on *Isogenoides**

John F. Hanson

For the loan of the material which made this study possible I am deeply indebted to Prof. N. Banks of the Museum of Comparative Zoology at Harvard University, to Dr. C. E. Palm and Dr. H. Dietrich of Cornell University, and to Dr. A. B. Gurney of the United States National Museum. Their kindly cooperation and the wealth of help and advice received from Dr. C. P. Alexander and Dr. G. C. Crampton of this department have made this project both interesting and profitable.

Isogenus was erected as a genus by Newman in 1833. In 1904 Klapalek split off the subgenus *Dictyogenus* on the basis of an apical network of crossveins of the wings. In 1912 he erected *Isogenoides* as a subgenus of *Isogenus* to receive some North American species with a "nail" on the posterior ventral margin of the seventh abdominal segment of the male. A reanalysis of these groups shows that *Dictyogenus*, like other Perlodid genera based on very superficial and highly variable wing venational characters, is not valid. The few individuals at hand show, as would be expected in the Perlodidae, that the number and position of apical crossveins varies to such a great extent that intermediates are numerous and the character cannot be used to define *Dictyogenus*. In addition, thoracic sclerites, mouthparts, and other head structures of *Dictyogenus* and *Isogenus* are identical and the genitalia also are of a single type. *Isogenoides*, however, exhibits some very fundamental differences. In the thoracic sternum of this group are generic characters which are even more distinct and unique than those found by Klapalek in the genitalia.

On the basis of these discoveries I am here synonymizing *Dictyogenus* under *Isogenus*; and to give *Isogenoides* its justified equal standing with related groups I am raising it to generic rank. *Isogenus* seems to be represented in North America by numerous species, placed in the literature in the genus *Perla*. Of *Isogenoides* there are a half dozen North American species known to me. Not a single one of these species, however, has been placed in its proper genus since the original work of Klapalek (1912). Needham and Claassen in their monograph placed them in *Isogenus*; Banks placed some in *Perla*; and Frison placed one in *Hydroperla*. More species of *Isogenoides* than are discussed here may eventually be recognized as already described and improperly placed in other genera of Plecoptera.

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Generic Characters

Figs. 9, 10

ISOGENUS Newman, 1833

1833. *IsoGENUS* Newman, Ent. Mag. 1:415.1904. *Dictyogenus* Klapalek, Ceska Akad. Cis. Fr. Jos. I, Trida 2:13(17):8. New Synonymy.

This genus is redefined here in order to point out, more clearly than has been done previously, its points of difference from *IsoGENOIDES*.

Submentum with a prominent basal lateral protuberance which is slightly membranous at tip, and thus might be construed as being gill-like. The thorax is entirely gill-less. For the details of ventral thoracic sclerites see Figure 9. Note that the furcasternum of meso- and metathorax is demarked from the basisternum by a suture. In the wings, apical crossveins are few or lacking; branches of Rs usually numerous (3 or more). Genitalia of male with distinct supraanal process; sometimes without lateral stylets. Tenth tergite split dorsally and bearing dorsal lobes or genital hooks.

ISOGENOIDES (Klapalek), 1912

1912. *IsoGENUS* (*IsoGENOIDES*) Klapalek, Collect. Zool. S. Longchamps 4(1):57.

Submentum with a pair of prominent basal membranous gills. Thorax entirely gill-less. For details of ventral thoracic structure see Figure 10. The mesothoracic furcasternal plate of this genus is unique in its suturing. A straight suture divides it along the longitudinal axis into two equal parts; a Y-shaped suture bounds it posteriorly; and a straight transverse suture demarks it anteriorly from the basisternum. The metathoracic furcasternum also is well demarked from the basisternum of this segment by a straight suture. Genitalia of male with distinct supraanal process and lateral stylets. Supraanal process usually elongate and strengthened by a posterior and an anterior sclerotized bar. "Nail" on the posterior margin of the seventh abdominal sternite present but sometimes very indistinct. Tenth tergite split dorsally, and bearing dorsal lobes or genital hooks posteriorly. Ninth sternite produced slightly posteriorly; without spinulae above.

In addition to being homogeneously grouped by the above-mentioned characters, the half dozen species of *IsoGENOIDES* are very similar in color, size, and mouthparts. The general color is dark brown; with distinct yellow markings on head and pronotum. Head mostly brown. Yellow occipital region not extending forward sufficiently to include the hind angles of the head behind the compound eyes. Post-ocular marmorations present, occurring in the dark pigmented region of the occiput. Transverse M-line usually darkened, especially conspicuous in pinned specimens because of absence of tiny setae which are present on the rest of the dorsal surface of the head. Often with conspicuous black areas around the lateral ocelli. A yellow spot usually present on the dorsal surface of the head near the base of each antenna. Pronotum with a

broad median yellow band, flanked by the brown disks bearing darker brown rugosities. Frison's (1937) figure of the color pattern of the head and pronotum of *I. varians* is very accurate and typical of every species in the genus except *I. dorata* which has a yellow spot in the interocellar space.

The males of *I. elongatus* only, are found to have a brachypterism to such an extent that the wings do not extend to the tip of the abdomen. In some cases a few apical crossveins occur, especially in *I. frontalis*; branches of Rs usually 3 in number.

Male genitalia offer excellent characters for distinguishing species. Significant differences are to be found in the dorsal lobes, the supraanal process, lateral stylets, and subanal lobes. The great amount of variation of the subgenital plate of females within a species sometimes limits possibilities of exact species identification in this sex.

KEY TO MALES OF ISOGENOIDES

1. Supraanal process with an apical, posteriorly directed hook. 2
 Supraanal process without an apical hook. 5
2. Apical hook of supraanal process membranous. Also bearing a pair of subapical hooks posteriorly. *I. elongatus*
 Apical hook darkly and strongly sclerotized. No subapical hooks on the posterior surface of the supraanal process. 3
3. Dorsal lobes of tenth tergite relatively large and with a very broad apex. Apical hook of supraanal process large. *I. dorata*
 Dorsal lobes elongate, and angulate on posterior margin near apex. Apical hook of supraanal process smaller. 4
4. Posterior margin of dorsal lobes sharply angulate near apex. Lateral stylets of supraanal process elongate. Subanal lobes large. *I. frontalis*
 Posterior margin of dorsal lobes obtusely angulate near apex. Lateral stylets short and tapering. Subanal lobes normal in size. *I. hudsonicus*
5. With a long lash-like appendage attached at the base of the supraanal process. Supraanal process with two apical, anteriorly directed spines. Lateral stylets with a sharp apex. *I. olivaceus*
 Not as above. Supraanal process grooved apically; with an anterior and a larger posterior pair of subapical spines or hooks. Lateral stylets with blunt apex. *I. varians*

KEY TO FEMALES OF ISOGENOIDES

1. Head with a spearhead of yellow pigment extending into the interocellar space. *I. dorata*
 Head without yellow pigment in the interocellar space. 2
2. Subgenital plate with a broad and usually deep median emargination. *I. hudsonicus*, and *I. frontalis*
 Subgenital plate not as above. 3
3. Subgenital plate projecting only slightly over segment nine; often with a small median notch. *I. elongatus*
 Subgenital plate often projecting one-half or more of the distance across segment nine; broad, with truncate or convex apical margin. 4
4. Subgenital plate with a truncate apical margin. *I. olivaceus*
 Subgenital plate with a median nipple-like protrusion on apical margin. *I. varians*

ISOGENOIDES ELONGATUS (Hagen), 1874

Figs. 6, 11, 12

1874. *Isogenus elongatus* Hagen ♀, U. S. Geol. and Geogr. Survey Terr. Rept. 1873: 576-577 (types at M.C.Z.).

1912. *Isogenus* (*Isogenoides*) Klapalek, Collect. Zool. S. Longchamps 4(1):58.

1925. *Isogenus* Needham & Claassen, Plecop. Amer. North of Mex., p. 71-72, figs. of ♂ ♀ gen.

This species was originally described by Hagen in 1874. Klapalek in 1912 correctly placed it in *Isogenoides*. The male sex of *elongatus* was first described by Needham and Claassen in 1925. However, their description is unrecognizable, and since they designated no allotype specimen I am here redescribing the male sex and designating types.

Length to tip of wings, 7 to 8 mm. in male, 22 to 26 mm. in female; length of body, 15 to 16 mm. in male, 16 to 18 mm. in female; length of fore wing, 4 mm. in male, 19 to 21 mm. in female.

Male.—Tenth segment of abdomen widely split above; dorsal lobes thumb-like, partly membranous, bearing a few spinulae and numerous short setae. Supraanal process elongate, with very distinct apical characters; at the very tip is a membranous, finger-like projection; further basad and on the posterior surface of the supraanal process are a pair of small, sharp, quite widely separated points. Lateral stylets darkly sclerotized, cylindrical at apex, becoming broader and thus flatter toward the base. When the supraanal process is retracted within its membranous sheath, usually only the tips of the lateral stylets are visible. Apical region of subanal lobes largely membranous.

Female.—The subgenital plate of the female is only slightly protrusile and usually has the tiny, median notch as drawn by Needham and Claassen (1925) (see Fig. 11). All three type females at the M.C.Z. have the notch. However, close examination of other specimens at hand shows that the median notch is sometimes absent (see Fig. 12).

Collection Data: Allotype, male.—Colorado (deposited at Harvard University in the Museum of Comparative Zoology). Parallotypes.—1 ♂ Platte Canyon, Colorado (Dyar & Caudell) in my personal collection. 1 ♂ Platte Canyon, Colorado, May (Dyar & Caudell) (U.S.N.M. type no. 56215). 1 ♂ Poudre R., Colo., June, 1889 (in Cornell Coll.). 1 ♂ Poudre R., Colo., June 1883 (in my coll.). Additional Records.—2 ♀ Beaver Dick Lake, Grand Tetons, Wyo., alt. 6850 ft., July 10, 1941 (W. Harrison). 1 ♀ data as above (C. P. Alexander). 1 ♀ Leigh Lake, Grand Tetons, Wyo., alt. 6875 ft., July 12, 1941 (C. P. Alexander). 2 ♀ Columbia River, near Peteros, Wash., May 27, 1929 (M. D. Leonard). 1 ♀ Poudre R., Colo., June, 1883.

ISOGENOIDES FRONTALIS (Newman), 1838

Figs. 3, 17, 18

1838. *Isogenus frontalis* Newman ♂ ♀, Ent. Mag. 5:178.

1874. *Isogenus colubrinus* Hagen ♀, U. S. Geol. and Geogr. Survey Terr. Rept. 1873:576 (types at M.C.Z. and in London). *New Synonymy*.

1912. *Isogenus frontalis* Klapalek, Collect. Zool. S. Longchamps 4(1):57-58, figs. of ♂ ♀ gen.

1918. *Perla titusi* Banks ♀, Bull. Mus. Comp. Zool. **62**:6, fig. 25 (synonymized by N. & C. in 1925).
1920. *Perla incesta* Banks ♀, *ibid.* **64**:318 (synonymized by N. & C. in 1925).
1925. *Isogenus frontalis*, *colubrinus* Needham and Claassen, Plecop. Amer. North of Mex., p. 69-71, 72-73, figs. inaccurate.

In a study of the types of *Isogenoides colubrinus* (Hagen), the figures of the types of *I. frontalis* drawn by Klapalek (1912), and a considerable series of materials from Cornell and the Museum of Comparative Zoology, it has become evident that *I. colubrinus* is a synonym of *I. frontalis*. Hagen was led to describe *I. colubrinus* probably because the female specimen on which the description is based has a subgenital plate greatly different from that of the type of *I. frontalis*, as later drawn by Klapalek. However, numerous specimens show these extremes to be easily encompassed by variations within the species; distribution also now indicates that they represent one and the same species.

Needham and Claassen, in their monograph, tried to retain *I. frontalis* as an eastern species and *I. colubrinus* as a western species. A reexamination of their material shows that they had intermingled two species because they missed the fundamental distinguishing characters to be found in the lateral stylets of the supraanal process and in the dorsal lobes of the tenth tergite. However, they were aware of and admitted their own confusion and inability to separate *frontalis* from *colubrinus*, by suggesting that the two probably would be found to be synonymous, and such is indeed the case. The actual distribution of the species extends across the entire continent in the transitional and lower Canadian zones. Another species which Needham and Claassen did not separate from this series of material is a very closely related more northern species (*I. hudsonicus* n. sp.) found across the continent in the upper Canadian and Hudsonian zones. That the former more southern species is *I. frontalis* is indicated by locality of the types (Trenton Falls, N. Y.) and is proven by Klapalek's (1912) drawing of the male showing the characteristic lateral stylets.

I have checked the types of *Perla titusi* and *P. incesta* Banks and agree, on the basis of subgenital plate and collection data, that Needham and Claassen were right in synonymizing them under this species.

Length to tips of wings, 12 to 22 mm. in male, 17 to 23 mm. in female; length of body, 14 to 17 mm. in male, 14 to 18 mm. in female; length of fore wing, 9 to 17 mm. in male, 14 to 19 mm. in female.

Male.—Dorsal lobes of tenth tergite boot-shaped, the "feet" of the two boots usually abutting directly against each other where they meet dorsally; bearing a few spinulae on the "feet." Supraanal process elongate, with a large, well sclerotized hook at apex. Lateral stylets well sclerotized, slightly flattened, slightly curved, and of nearly uniform width throughout their length; tips sometimes visible when supraanal process is retracted. Subanal lobes relatively large and with only a very small amount of membranization apically.

Female.—Subgenital plate of female variable but always with a median notch. The range of variation is even greater than that indicated by the figures

(labelled *Isogenus frontalis* and *I. colubrinus*) of Needham and Claassen (1925) (see Figs. 17, 18).

Collection Data—A considerable number of specimens of this species from Harvard and from Cornell have been studied. Since published distributional data are based on determinations which are in large part inaccurate, I am including here the records of all of these specimens, as I have redetermined them, in order to present data that will show correctly the distribution of the species.

The data immediately below are recorded from specimens in the Cornell Collection. 2 ♂, Niagara Falls, N. Y., June 24, 1901. 3 ♂, Apostle Islands, Ashland Co., Wisc., July 7, 1907. 1 ♀, Apostle Islands, Ashland Co., Wisc., July 8, 1907. 1 ♀, Lawrence, Kansas. 1 ♂, 1 ♀, Edmonton, Alta., June 7, 1925 (Owen Bryant). 1 ♀, Edmonton, Alta., May 28, 1925 (O. Bryant). 1 ♂, Banff, Alta., July 23, 1925, (O. Bryant). 1 ♀, Jackson Hole, Wyo., alt. 6700 ft., July 25, 1929 (E. Klots). 2 ♀, Rifle, Colo., June 23, 1904. 1 ♀, Kenosha Pass, Colo., August (Osler). 1 ♂, 1 ♀, Moscow, Idaho (J. M. Aldrich). 1 ♂, Lewiston, Idaho (C. V. Piper). 1 ♀, Clifton, Ariz., March 22, 1918 (J. I. Carlson). 1 ♂, Carbonata, B. C., July 6-12. 1 ♂, Pullman, Wash., May 29, 1897. 1 ♂, Pullman, Wash., May 18, 1908. 1 ♀, Camp Umatilla, Wash., June 27, 1862 (S. Henshaw). 8 ♂, 4 ♀, Columbia River, Peteros, Wash., May 27, 1929 (M. D. Leonard). 1 ♂, Umatilla, Or., June 24, 1882 (S. Henshaw). 2 ♂, 2 ♀, The Dalles, Or., June 23, 1882 (S. Henshaw). 1 ♂, 1 ♀, Umatilla, Or., June 24, 1882 (S. Henshaw). 1 ♂, Corvallis, Or., April. 1 ♀, Corvallis, Or., May 8, 1929 (V. T. Shattuck). 1 ♀, Corvallis, Or., April 6, 1932 (Virgil Starr). 1 ♀, Corvallis, Or., March 21, 1932. 1 ♀, Corvallis, Or., March 26, 1931 (Jas. Roaf). 1 ♂, Elkton, Or., March 26, 1896.

The data listed below are recorded from specimens in the M.C.Z. at Harvard. 1 ♀, Niagara Falls, June. 1 ♂, Lewiston, Idaho (C. V. Piper). 2 ♀, Ohio (Schaum). 1 ♂, Vancouver, B. C. (R. V. Harvey). 1 ♀, Wawawai, Wash. (C. V. Piper). 1 ♀, Wash. Exp. Sta., E. Wash. 1 ♂, 1 ♀, Wash. Exp. Sta., Alnota, Wash. 1 ♂, 2 ♀, The Dalles, Or., June 22, 23, 1882 (S. Henshaw). 3 ♂, 2 ♀, Umatilla, Or., June 24, 1882 (S. Henshaw).

The following data are based on two females in the U.S.N.M. doubtfully placed as this species. 2 ♀, Kokanee Mtn., B.C., alt. 9000 ft. August 10, 1903 (R. P. Currie) (collected on snow).

The following specimen is deposited in the Massachusetts State College Collection. 1 ♀, Beaver Dick Lake, Grand Tetons, Wyo., alt. 6850 ft., July 10, 1941 (C. P. Alexander).

Isogenoides hudsonicus n. sp.

Figs. 7, 17, 18

1925. *Isogenus frontalis*, *colubrinus* Needham & Claassen, *Plecopt. Amer. North of Mex.*, p. 69-71, 72-73. (In part.).

As mentioned under *I. frontalis*, I discovered specimens of this new species intermingled with Needham and Claassen's material of *I. frontalis* and *colubrinus*.

The head color pattern of this species does not differ from that described previously in this paper for the genus as a whole.

Length to tip of wings, 14 to 15 mm. in male, 17 to 20 mm. in female; length of body, 12 to 15 mm. in male, 14 to 18 mm. in female; length of fore wing, 12 to 14 mm. in male, 15 to 16 mm. in female.

Male.—Dorsal lobes of tenth tergite slender, finger-like, angulate near the middle, bearing several spinulae. Supraanal process elongate, with a heavy

hook at the apex. Lateral stylets short, tapering from a broad base to a blunt apex; tips not visible when supraanal process is retracted. Subanal lobes with a small membranous apical region.

Female.—Subgenital plate similar to that of *I. frontalis* (see Figs. 17, 18).

Collection Data.—Holotype male, allotype female—Ungava Bay, Hudson Bay Territory, Canada (L. M. Turner) (Cornell U. Type No. 1794). Paratypes.—1 ♀, Kuni-bal?, Newfoundland. 2 ♂, Grand Lake, Newfoundland, July 28, 1916. 4 ♂, 1 ♀, Grand Lake, N.F., July 25. 3 ♂, Grand Lake, N.F. 1 ♂, Grand R., Can., July 1, 1888 (L. Cabot). 1 ♂, 2 ♀, Ungava Bay, H.B.T., Can., (L. M. Turner). 1 ♂, 1 ♀, Ungava Bay, H.B.T., Can. (L. M. Turner) (U.S.N.M. type no. 56214). 1 ♂, Great Slave Lake, Can. 1 ♂, 2 ♀, Winnipeg Lake, Can., 1860 (Kennicott). 1 ♂, 2 ♀, Saskatchewan, Hudsonia, Can., 1860 (Kennicott). 1 ♀, Ft. Yukon, Alaska. 1 ♀, Dawson City, Yukon, Terr., Can., Sept. 5, 1912 (J. M. Jessup) (U.S.N.M. type no. 56214). Types are deposited at the M.C.Z., at Cornell, and in my personal collection.

In the male sex this species is easily distinguished from its closest ally, *I. frontalis*, on the basis of several characters. The dorsal lobes are shorter and of a different shape than in *I. frontalis*. The supraanal process is longer and bears a larger apical hook. The lateral stylets also are longer than in *I. frontalis*. The females of the two species cannot be distinguished.

ISOGENOIDES OLIVACEUS (Walker), 1852

Figs. 1, 2, 13, 16

1852. *Perla (Isogenus) olivacea* Walker ♂, Cat. Neur. Ins. Brit. Mus., Pt. I, p. 144.
1912. *Isogenus (Isogenoides?)* Klapelek, Collect. Zool. S. Longchamps 4(1):59-60, fig. of ♂ gen.
1938. *Perla olivacea* Ricker ♀, Trans. Roy. Canad. Inst. 22:142-143, sketch figs. of ♂ ♀ gen.

This species is extraordinary in the characters of its male genitalia. Although Ricker's drawings are sketchy they show the unmistakable whip-like projection of the supraanal process. I have redrawn the genitalia of this species in this paper to point out several other good specific characters. Due to its peculiarly appearing genitalia, the generic status of this species has been unsettled, but I find that the ventral sclerites unmistakably place it in *Isogenoides*.

The head color pattern is as described for other species of *Isogenoides* except that, as noted by Ricker, the black rings on the inner sides of the ocelli are usually more conspicuous than in other species.

Length to tip of wings, 14 to 15 mm. in male, 18 to 20 mm. in female; length of body, 12 mm. in male, 14 to 15 mm. in female; length of fore wing, 12 mm. in male, 15 mm. in female.

Male.—Dorsal lobes of tenth tergite large, broadly rounded at tip, partly membranous, covered with numerous long setae and with several spinulae on the sclerotized portion. Supraanal process remarkably modified: main portion largely membranous but with a supporting sclerotized plate or bar; bifid into two sharp, anteriorly projecting and slightly curved tips; with a curious lash extending posteriorly from the base of the main piece. Below the base of the

lash is a conspicuous sclerotized plate on either side of which lie the lateral stylets. These are small but darkly sclerotized, flat, and curved to a sharply pointed apex. Subanal lobes moderately large, with the lower half membranous, bearing numerous long setae.

Female.—The subgenital plate apparently varies considerably. Ricker figures that of the allotype as being emarginate. I have studied a specimen from the M.C.Z. which does not have an emarginate subgenital plate but one which is truncate at the apex (see Fig. 16).

Collection Data.—1 ♂, 1 ♀, Michipicoten Bay, Lake Superior, Ontario, Canada, 1862 (G. Barnston) (at M.C.Z.).

ISOGENOIDES VARIANS (Walsh), 1862

Figs. 5, 19

1862. *Perla varians* Walsh ♂ ♀, Proc. Acad. Nat. Sci. Phila. 13:364.

1925. *Perla varians* Needham & Claassen, Plecop. Amer. North of Mex., p. 83-84, poor figs. of ♂ ♀ gen.

1935. *Hydroperla varians* Frison ♂, Ill. Nat. Hist. Survey Bul. 20:426-427, good figs. of ♂ gen. New Synonymy.

1937. *H. varians* Frison ♀, nymph, Ill. Nat. Hist. Survey Bul. 21:82-83, good figs. of head and pronotal color pattern and ♀ subgenital plate. New Synonymy.

This species was originally described by Walsh from eleven specimens, male and female. It appears that Needham and Claassen may well have had some other species at hand when describing *P. varians* in their monograph. Frison studied a male specimen from the M.C.Z. which he figures and describes (1935) as *Hydroperla varians*. A study of one of Walsh's types, deposited at the M.C.Z., proves that his association is correct. However, his placement of the species in the very weak genus *Hydroperla* is incorrect. It is definitely placeable, on genitalic, thoracic, and wing characters, in *Isogenoides*. I am here designating the male type of Walsh, deposited at the M.C.Z., as lectotype.

Length to tip of wings, 15 to 17 mm. in male, 17 to 21 mm. in female; length of body, 13 to 15 mm. in male, 13 to 18 mm. in female; length of fore wing, 14 mm. in male, 15 to 17 mm. in female.

Male.—Dorsal lobes of tenth tergite flat, bluntly pointed, covered with long setae, and bearing a small region of a few spinulae anteriorly. Supraanal process elongate, with a distinct groove and not a hook at the apex, bearing a pair of spines on the posterior surface near the apex and a smaller pair of spines anteriorly a little farther basad. Lateral stylets short and blunt, not visible when supraanal process is retracted. Subanal lobes short and broad, with a large membranous region at apex.

Female.—In all specimens examined I have found the subgenital plate to be considerably different from that shown by Frison (1937) (see Fig. 19). This of course is a range of variation that might very well be expected in Plecoptera.

Collection Data. Lectotype, male.—"Type 10128, Rock Island." 2 ♂, Port Huron, Mich., June (H. G. Hubbard) (at U.S.N.M.). 2 ♀, Port Huron, Mich., June (Hubbard and Schwarz) (at U.S.N.M.). 1 ♀, Port Huron, Mich., June (Hubbard and Schwarz) (at Cornell). 1 ♀, Port Huron, Mich., (at M.C.Z.).

A series of males and females borrowed from Cornell, labelled "student collection" but without other data, possibly indicated that the species also occurs in New York.

ISOGENOIDES DORATA (Frison)

Figs. 4, 8, 14, 15

1942. *Hydroperla dorata* Frison ♂ ♀, Ill. Nat. Hist. Survey Bul. 22:295-296, fig. 66 of ♂, ♀, naïad.

Almost to the time of printing of this paper *I. dorata* (Frison) has been included here as a new species. However, in a recent publication Frison has described the species in the genus *Hydroperla*. For the reasons pointed out in the appendix at the end of this article his assignment of this species to *Hydroperla* is incorrect.

Since the description of this species as included here offers important information supplementary to Frison's original description, I am retaining it in this article without change except of course that type designations must now be omitted.

The head color pattern is like that typical of the entire genus except that in this species there is a median projection of the occipital yellow area extending into the ocellar space (Fig. 8).

Length to tip of wings, 16 to 17 mm. in male, 22 to 24 mm. in female; length of body, 13 to 15 mm. in male, 15 to 19 mm. in female; length of fore wing, 13 to 15 mm. in male, 18 to 20 mm. in female.

Male.—Dorsal lobes large, broadly rounded at apex, closely covered with very long setae, and bearing a few exceptionally long spinulae. Supraanal process elongate, and with an unusually large apical hook. Lateral stylets similar to those of *I. frontalis*; slightly curved, slender, and of uniform width throughout. Subanal lobes short and blunt, membranous along lower margin.

Female.—Subgenital plate variable: sometimes evenly rounded, sometimes more nearly rectangularly produced (see Figs. 14, 15); usually extending about half way across segment nine.

Collection Data.—3 ♂ 2 ♀ Amherst, Mass., April 19, 1938 (Hanson); 4 ♂ (Bartlett); 2 ♂ April 22, 1942 (Hanson); 1 ♀ April 20, 1942 (Field). 2 ♂ 3 ♀ Gatlinburg, Tenn., April 2, 1941 (Hanson).

This species is readily distinguished from all other known species of *Isozenoides* by the spearhead of yellow pigment extending into the ocellar space. The female may well be confused with other species, such as *varians* or *olivaceus*, on the character of its subgenital plate, but the male is easily distinguished by the dorsal lobes on the tenth tergite, the supraanal process, and the lateral stylets (see figures of males).

Appendix

Since the preparation of this paper some time ago, Frison has published (September 1942) a long article concerning various phases of stonefly taxonomy. In the article presented here and the preceding one of this series there are numerous observations that are at variance with those of Frison which are published in the above-mentioned paper and which need clarification. Since this paper was already in the hands of the editor at the time of the preparation of these supplementary notes, my comments are added here in the form of an appendix. The only change in the text of the paper itself concerns the last species discussed, *I. dorata* (Frison). This species had originally been included here as new but Frison has described it as a new species in the genus *Hydroperla* in the above-mentioned paper.

ISOGENOIDES FRONTALIS Newman

Isogenoides must be recognized as a genus entirely distinct from *Isogenus* on the basis of unique generic features discussed on a previous page of this article. *I. frontalis* belongs in the genus *Isogenoides*.

Frison's synonymy of *I. colubrinus* under *I. frontalis* is correct although his reasons for this action are not correct. As mentioned under my discussion of *hudsonicus* the females of the latter species and of *frontalis* are indistinguishable. Thus since there are two species indistinguishable in the female sex, and since *colubrinus* was described from females alone, it is not possible to synonymize the latter under *frontalis* on the basis of anatomical identity alone. However, as I have pointed out in the text of this paper it is possible to synonymize *colubrinus* under *frontalis* on the basis of geographical distribution and anatomical identity. Examination of numerous males from many localities shows that the types of both *colubrinus* and *frontalis* were taken within the range of a single species (*I. frontalis*). Furthermore, the other species (*I. hudsonicus* n. sp.) with which *frontalis* might be confused is not known to occur within the same range since it is a much more northern species (see collection data under that species). On this basis alone *colubrinus* can be considered as a synonym of *frontalis*. It is difficult to determine whether Frison has figured the male of *frontalis* or of *hudsonicus* since he does not show in detail the two most diagnostic characters, i.e. the length of the lateral stylets and the distinctive shape of the dorsal lobes of the tenth tergite. It is probable, however, that his figures were drawn from specimens of *frontalis* since all except one of the specimens that he lists in his distributional data are probably correctly identified as *frontalis*. The female that he records from Newfoundland is probably *hudsonicus* and not *frontalis*.

HYDROPERLA Frison

The genus *Hydroperla* as used by Frison appears to be of dubious value. The genus is based on wing and genital features which, as is well known, frequently prove highly variable in Plecoptera. A study of other structures,

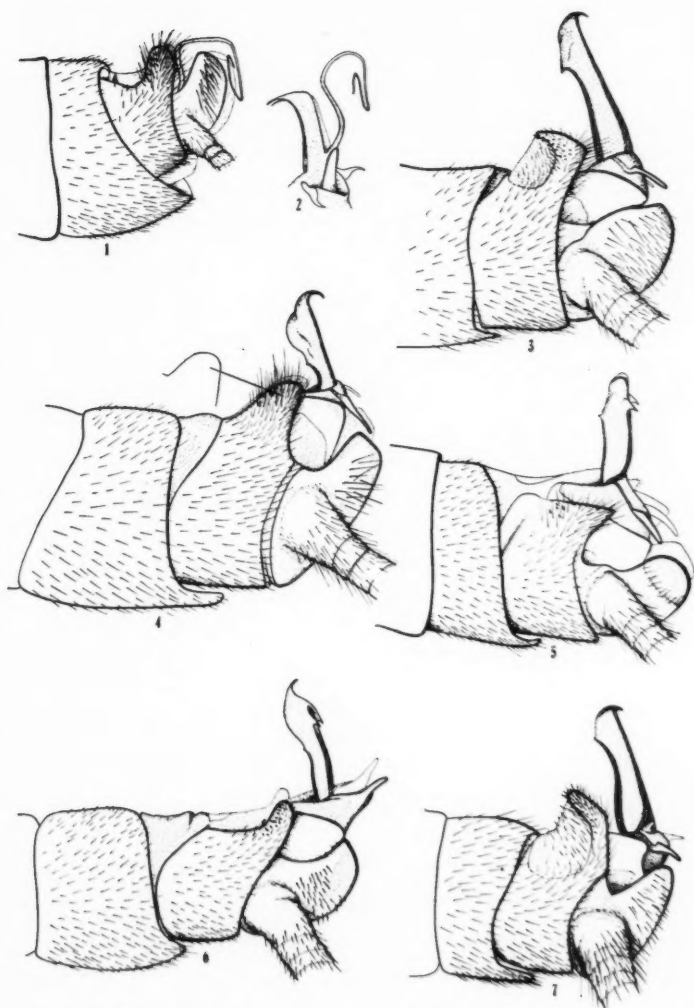


PLATE 1: Terminalia of Males of *Isogenoides*. Figs. 1 and 2, *I. olivaceus* (Walker). 3, *I. frontalis* (Newman). 4, *I. dorata* (Frison). 5, *I. varians* (Walsh). 6, *I. elongatus* (Hagen). 7, *I. hudsonicus* n. sp.

particularly the thoracic sternum, makes it entirely obvious that there is a considerable amount of taxonomic confusion among the several species that have been placed in *Hydroperla*. Its type species *Perla crosbyi* N. & Clns. may well belong in *Isogenus* s. s. as it closely resembles the genotype *Isogenus nubecula* Newman in morphological features. A definite decision on this matter awaits further detailed study. The species *varians* which Frison placed in *Hydroperla* is obviously an *Isogenoides* on the basis of its numerous identi-

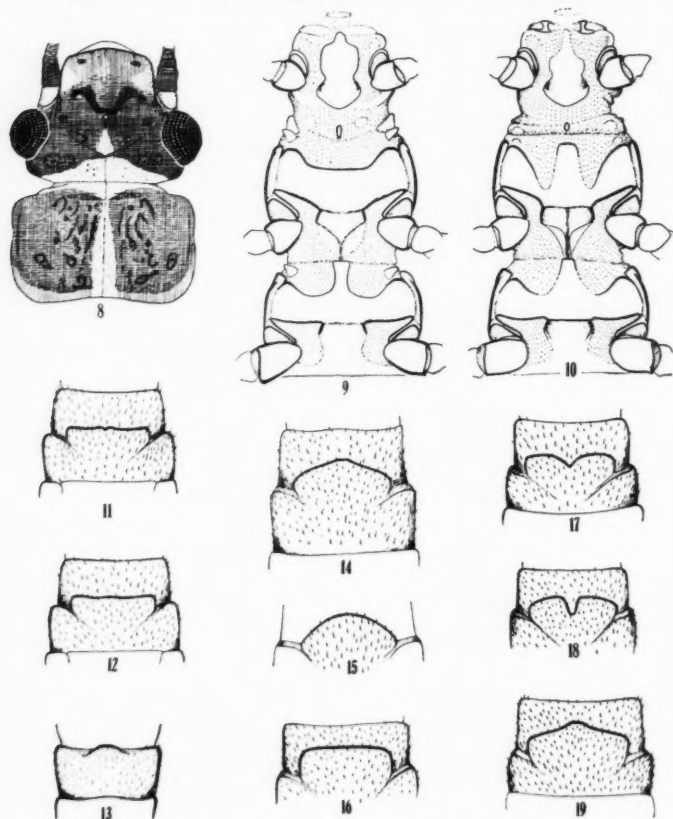


PLATE 2: Fig. 8, *Isogenoides dorata* (Frison), head and pronotal color pattern. 9, *Isogenus* Newman, thoracic sternum. 10, *Isogenoides* (Klapalek), thoracic sternum. 11 and 12, *Isogenoides elongatus* (Hagen), ♀ subgenital plate. 13, *I. olivaceus* (Walker), seventh sternite of ♂. 14 and 15, *I. dorata* (Frison), ♀ subgenital plates. 16, *I. olivaceus* (Walker), ♀ subgenital plate. 17 and 18, *I. frontalis* (Newman) and *I. hudsonicus* n. sp., ♀ subgenital plates. 19, *I. varians* (Walsh), ♀ subgenital plate.

fying structures (see notes on *Isogenoides* in the text of this paper). In similar manner, the species *olivacea* and *dorata* definitely are members of the genus *Isogenoides* and not of *Hydroperla*. Frison's species *Hydroperla parallela* is really an *Arcynopteryx* and is a synonym of *Arcynopteryx americana* Klapalek (see Part II of this series in Amer. Midl. Nat. vol. 28, no. 2).

PROTARCYS DOLOBRATA Smith

As has been shown in Part II of this series the "lumping" of several North American genera under *Perlodes* is entirely unjustified although most American workers have done this. The species *P. dolobrata* is given full specific rank by Frison. I would point out however, the similarity of his figures of the type of *dolobrata* to my figures of the male of *tibialis* as evidence of the true status of *dolobrata*. Such a comparison makes evident the fact, as I have pointed out in my paper published simultaneously with Frison's, that *dolobrata* is a synonym of *tibialis*.

PROTARCYS BRADLEYI Smith

Frison has not figured the male of *bradleyi* in his recent paper but by my figures (1942, Figs. 26a and 26b) it is obvious that this species cannot be synonymized under *tibialis*. In addition to genitalic differences there are differences in the head color pattern particularly in the ocellar region that prove that *P. tibialis* and *P. bradleyi* are two distinct species (see Figs.)

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Studies on the Life History and the Ecology of the Hothouse Millipede, *Orthomorpha gracilis* (C. L. Koch 1847)¹

Nell Bevel Causey

The very wide distribution of the hothouse millipede has resulted in a somewhat complicated synonymy. Some recent authors (Williams and Hefner 1928, Loomis 1939) have followed Cook (1911) in treating it as the type of the genus *Oxidus*, but most writers still refer it to the genus *Orthomorpha* (Attems 1930, Verhoeff 1928, Chamberlin 1939).

Weber (1882) reported the presence of free hydrocyanic acid in the secretion from the repugnatorial glands of the hothouse millipede. McDaniel (1931) made a brief reference to its life history. Other references to this millipede have been concerned with its morphology and distribution; the most detailed is that of Cook (1911).

Like other polydesmid millipedes, *Orthomorpha gracilis* is flattened dorso-ventrally. The keels or carinae are nearly horizontal and less than one-fourth the width of the body cavity. The 20 post-cephalic somites bear 30 or 31 pairs of legs, depending upon whether the specimen is a male or a female. The gonopods, a pair of highly modified walking appendages present only in adult males, are on the seventh post-cephalic somite between the seventh and eighth pairs of legs. Each gonopod (Fig. 1) is composed of a prominent basal joint and an apical joint with a short cushion-like hirsute base, a stout, slightly curved shaft, and four terminal curved prongs. Male specimens vary between 18.5 and 19.9 mm. in length and 2.0 and 2.2 mm. in width; female specimens vary between 19.4 and 22.2 mm. in length and 2.0 and 2.5 mm. in width. Recently moulted specimens are creamy white, but before they leave the moulting chamber the color may change to light brown. In the oldest specimens the dorsum is a deep chestnut brown or black, the keels are bordered with lemon yellow, the sides are chestnut brown, the sterna and basal joints of the legs are pallid, the distal joints of the legs and the apex of the body are light brown, and the antennae and vertex are dark brown. Immature specimens of the later stadia, which greatly outnumber mature specimens in most collections, resemble the latter closely in shape, but are easily distinguished by their smaller size, paler color, absence of mature gonopods, and smaller number of post-cephalic somites. Stadia I and II are shown in figures 2 and 3.

Geographical Distribution

Many species of millipedes are localized in areas which are very limited in extent. Some have attained a wide distribution in the tropics, however, and a

¹ Research Paper No. 763, Journal Series, University of Arkansas.

few, of which *Orthomorpha gracilis* is an outstanding example, have entered temperate regions by way of the congenial conditions in greenhouses.

Since this millipede was first described from a greenhouse in Austria it has been reported from many tropical lands and islands, numerous hotbeds and greenhouses, and a few caves in temperate climates. From its original habitat in the East Indies (Cook 1911), it has spread so far that it is the most common and widely distributed representative of the Class Diplopoda (Attems 1899, Cook 1911). It occurs widely in European greenhouses (Koch 1847, Weber 1882, Attems 1899) and in the southern Mediterranean area (Verhoeff 1928). There is one indefinite record of it in Asia (Brölemann 1909). It has been reported from St. Thomas Island, New Zealand, Viti Islands (Attems 1930), Borneo, Samoa, Malasia, Olinda (Brölemann 1909), Great Loo Choo (Pocock 1895), and the Antilles (Latzel 1884).

Orthomorpha gracilis appears to be widespread in Mexico (Saussure 1860, Humbert and Saussure 1872) and in South America. It was reported from Rio de Janeiro, Santos, São Paulo, Paraná, Cubatao, Guatemala, Belém, Piquete, Santa Rita, Valparaíso and the following islands: Fernendo Noronha, Magarita, Dominican Republic, and the Bermudas (Brölemann 1909, Attems 1899). It was not one of the 67 species of diplopods collected in Colombia, British Guiana, St. Croix, and the United States Virgin Islands in 1913 and 1914 (Chamberlin 1923), nor was it listed among 150 species of diplopods from the West Indies (Chamberlin 1918) and 78 species of millipedes from northeastern Peru (Chamberlin 1941).

In North America *Orthomorpha gracilis* is known to occur in greenhouses throughout Maryland (Bollman 1893), Kansas (Gunthorp 1913), western Ontario (Gibson and Ross 1920), New York (Bailey 1928), Ohio (Miley 1927, Williams and Hefner 1928), Michigan (McDaniel 1931), North Carolina (Brimley 1938), and Arkansas. Further study will probably show that it is distributed generally in greenhouses in the United States and Canada. It occurs in the open in southern Ohio (Williams and Hefner 1928), southern California and other warmer parts of this country (Chamberlin 1939, personal letter), and in North Carolina. It was present in one cave in Pennsylvania, but in none of the 59 other caves in seven eastern states from which Mr. Kenneth Dearolf collected invertebrates (Loomis 1939).

Methods

The hothouse millipedes used in this study were collected from the greenhouses of Mr. C. N. Hibberd, Durham, North Carolina. They were present in numbers as great as 359 to a square foot in heavily manured soil on the tables where biennials were growing. They were less numerous on tables on which flower pots were set in cinders and under objects on the ground under the tables. The temperature in the greenhouses is kept above 22°C. Plants are thoroughly watered every day, and water drains from the tables rapidly. All collections were made during daylight hours. Greenhouse attendants reported that the millipedes come out upon the tables in large numbers at night. During

the day they were usually found under flower pots and large lumps of manure, loam, or cinders, but occasionally adults and older larvae were found moving about on the surface if the plant growth above them was thick enough to shade them from direct light.

The millipedes were brought from the greenhouses to the laboratory in jars or bottles and immediately transferred to finger bowls that contained loam, leaf mold, and manure from the greenhouses. If the substratum was kept moist and contained sufficient humus they lived several months. Too much water and too little air were fatal, but younger larvae were less susceptible to the harmful effects of these conditions than older larvae and adults. The millipedes under observation were kept in small finger bowls and in 50 cc. flat bottom flasks.

Experiments were carried out under the following temperature conditions: (1) a heated laboratory in which the temperature was around 22°C . during the day; (2) a warm air chamber in which the temperature fluctuated between 29° and 31°C .; (3) an unheated room in which the temperature fluctuated between 12° and 20°C .; (4) a refrigerator room in which the temperature control was set for 3.5°C .; and (5) boxes buried in the ground in the Duke Forest that were subject to ordinary outdoor variations in temperature between October, 1939, and April, 1940.

The amount of food that adults and larvae of the seventh stadium ate under the first four temperature conditions listed in the preceding paragraph was determined in the following manner: ten specimens of each of the last two

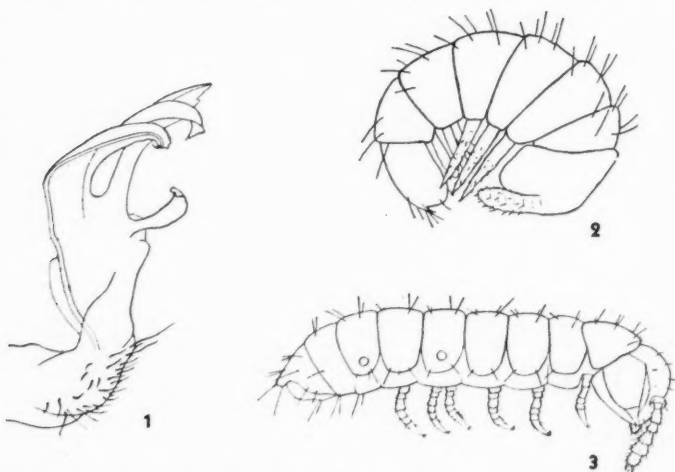


Fig. 1. Lateral view of right gonopod. Fig. 2. A larva of the first stadium. Fig. 3. A larva of the second stadium. (All figures $\times 140$).

stadia were placed in 50 cc. flasks that contained only (1) sterilized moist sand, (2) well-rotted manure from the greenhouses, (3) leaf mold, or (4) sterilized loam. The feces were collected and weighed daily for five days.

The toleration of adults and larvae of the seventh stadium to various conditions of humidity was determined in the following manner: two specimens of each of the last two stadia were put into vials that were suspended in screw-lid jars which contained supersaturated solutions of certain chemical compounds. The chemicals used had the following theoretical relative humidity values: H_2O , 100; $ZnSO_4$, 90; $NaCl$, 76; $NaHSO_4$, 51; $CaCl_2$, 32; $LiCl$, 14; $CaCl_2$ (dry), 0 (Sweetman 1933). The millipedes were allowed to remain in the tightly closed jars one hour at room temperature; then the jars were heated slowly in a water bath so that the temperature inside the jars rose one degree in five minutes. The temperature at which a millipede first appeared to be dead was recorded; then it was removed and cooled on wet filter paper so that it might recover if it was not really dead. The effect of low temperatures was determined by placing the millipedes in the refrigerator room for varying lengths of time.

Life History

All diplopods are anamorphic, i. e., the larvae pass through a number of molts, during each of which the number of legs and post-cephalic somites is increased. Additional legs and somites are added in the embryonic region between the anal somite and the somite that was last formed. Polydesmids, polyzenids, and ascospormorphs pass through seven larval stadia, in each of which the number of leg pairs and somites is constant for the species or the group. Julids also normally pass through seven larval stadia, but after the first or second the number of legs and somites is not constant for the species. In the glomerids development is hemianamorphic, i. e., a series of anamorphic molts is followed by three molts which are unaccompanied by increases in the number of legs and somites (Verhoeff 1928).

Various phases of the following other polydesmid millipedes have been described: *Polydesmus complanatus* (Fabre 1855), *Polydesmus illyricus* (Latzel 1884, Verhoeff 1894), *Polydesmus abchasius* (Lagnau 1911), and *Euryurus erythropygus* (Miley 1927). The post-embryonic development of *O. gracilis* is similar to that of other polydesmids, but differences have been found.

Breeding habits.—McDaniel (1931) reported that the one annual generation of hothouse millipedes in Michigan greenhouses was from eggs that were produced in the spring. In Durham, North Carolina, greenhouses the writer found copulating pairs from May through June and from September through April. Eggs were collected from September through March, when it became necessary to discontinue collections. No collections were made during the summer months, but it is quite certain that eggs were produced then because of the young larvae that were collected in September. During the fall and winter months the millipedes copulated in cultures that were kept in the laboratory and in the unheated room.

Before copulation a male hothouse millipede transfers spermatic fluid to his gonopods in the following manner: the thorax is bent ventrally so that the openings of the vasa deferentia, which are on the third body somite, are in contact with the gonopods on the seventh somite. A drop of spermatic fluid is then transferred from the vasa deferentia to the gonopods, where it is held by the many short setae on the basal joint (Fig. 1). From the gonopods the spermatic fluid is transferred to the vulvae of the female. Fertilization is internal (Fabre 1855).

During copulation the position of the male and female is as follows: the ventral surface of the posterior 13 or 14 body somites of the male is parallel and dorsal to the anterior 10 or 11 body somites of the female; the legs of the male on those somites are bent closely around the female; in the region of the eighth, ninth, and tenth somites the body of the male is twisted half around the female so that his gonopods are in contact with the female's vulvae, which open on the third body somite. The head and thorax of the male are directed anteriorly and bent over the head of the female, which is held by the seven anterior pairs of legs of the male. Bright light or handling usually causes a pair to separate. Copulation of a pair may occur several times and it may last several hours.

The ratio of adult males to females collected over a period of several months was approximately two to three. Of the 223 adult specimens in three collections, 39 per cent were males and 61 per cent were females. In the same three collections, of the 285 larvae of the seventh stadia, 45.4 per cent were males and 54.6 were females. Of the 121 larvae of the sixth stadia, 46.3 per cent were males and 53.7 were females. Beginning with the fourth instar the sex of the millipede can be determined easily by the presence of one more pair of legs on the female than on the male.

In October, 1939, 13 pairs of copulating hothouse millipedes were isolated in the laboratory in fingerbowls containing moist loam and manure from the greenhouses. Eleven of the females died from one to 12 days after the last observed copulation. The males died from one to 19 days after the last observed copulation. Only one clutch of eggs was produced by these millipedes; a female observed copulating October 20 produced eggs from which the young emerged November 1. Since the longest incubation period observed for eggs at room temperatures was nine days, it is probable that the eggs were produced October 21. All of the females were examined after their death; in 11 of the 13 there were eggs in the oviducts almost as large as mature eggs.

Oviposition and Incubation of the Eggs.—The females deposit their eggs in small rough cavities from 3 to 15 mm. below the surface of the soil. In neither the greenhouses nor in the laboratory cultures were there found any indications of brooding bells or chambers that many polydesmids construct, nor did the females remain with the eggs during the incubation period as colobognath millipedes do. Eggs were collected from September through March. The variety of post-embryonic stadia collected in April and May and from September through April indicated that oviposition may occur during any

month of the year under favorable greenhouse conditions. This absence of a regular annual breeding season is characteristic of many tropical species of animals.

The eggs are creamy yellow or occasionally brown, spherical or subspherical, quite smooth, and coated with a glutinous fluid which causes them to adhere in clusters. They are rich in yolk in a semi-fluid state and are surrounded by a slightly tough envelop that consists of a vitelline membrane and a chorion (Korschelt and Heider 1899). The diameter is from 0.35 to 0.40 mm. and the length from 0.40 to 0.41 mm.

One clutch of approximately 300 eggs was found in the greenhouse. Other clutches of 151, 63, 52, 17, and 42 eggs were deposited by millipedes in laboratory cultures.

None of the eggs that rested on glass in a chamber where the theoretical relative humidity was 100 developed, but those under similar conditions but on wet filter paper did hatch. Eggs on wet filter paper at a temperature of 3.5°C. did not develop. Eggs in the laboratory on a substratum of moist paper or soil hatched in from 5 to 6, 4 to 6, 6 to 8, and 9 to 10 days after they were discovered. All were under approximately the same temperature and humidity conditions. No female was found ovipositing, so the exact dates of the deposition of the eggs are unknown. The small size of the eggs and the fact that they are deposited in cavities in the soil rather than in brooding chambers makes them difficult to discover. The writer is fairly certain, however, that the eggs of one clutch hatched in either nine or ten days after oviposition.

Post-embryonic Development.—The post-embryonic development of larvae reared from eggs and from larvae collected in the greenhouses was followed in the laboratory. The substratum in the fingerbowls in which they were kept consisted of a moist mixture of loam, leafmold, and manure from the greenhouses.

TABLE 1.—Number of Post-cephalic Somites, Number of Pairs of Legs, Location of Legs and Anus (A), and Mean Length of Ten Individuals of Both Sexes of Each Stadium in the Life History of *Orthomorpha gracilis*.

Stadium	No. Post-cephalic Somites		Pairs of Legs on Each Post-cephalic Somite																				Length in Mm.
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
I	7	3	0	1	1	1	0	0	A														0.51
II	9	6	0	1	1	1	2	1	0	0	A												1.55
III	12	11	0	1	1	1	2	2	2	2	0	0	0	A									3.60
IV	15	16	0	1	1	1	2	2	1	2	2	2	2	2	0	0	0	A					4.15
		17	0	1	1	1	2	2	2	2	2	2	2	2	0	0	0	A					4.61
V	17	22	0	1	1	1	2	2	1	2	2	2	2	2	2	2	0	0	A				4.82
		23	0	1	1	1	2	2	2	2	2	2	2	2	2	2	0	0	A				5.67
VI	18	26	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	0	A			7.41
		27	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	0	A			7.80
VII	19	28	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	0	A			12.43
		29	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	0	A			13.20
VIII	20	30	0	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	0	A		19.25
		31	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	0	A		20.82

The post-embryonic development of *Orthomorpha gracilis*, as summarized in Table 1, is characterized by seven molts, during each of which the transition from one stadium to the next occurs. Sexual maturity is reached in the eighth stadium. The larvae of each stadium differ in number of somites and legs, size, and amount of pigment, but the only larvae that differ greatly in appearance from the adults are those of the first stadium.

The first instar larvae lie almost motionless with the posterior post-cephalic somites and the head bent ventrad. There are seven post-cephalic somites; the second, third, and fourth bear one pair of legs each; the fifth bears two pairs of limb buds and the sixth one pair. The head is relatively larger than it is at any other stage. The antennae and legs are sparsely covered with minute setae, and a few larger setae are on the head and body (Fig. 2). This stadium lasted from 18 to 24 hours.

During the first molt the number of post-cephalic somites is increased to nine and the number of legs to six pairs. The second, third, fourth and sixth somites bear one pair of legs each and the fifth two pairs. The second instar larvae become active after the first day and move away from the spot where they emerged from the eggs. The yolk plates which were visible in the first stadium are no longer present, and the larvae begin feeding on tiny bits of organic matter in the soil. This stadium (Fig. 3) lasted from 11 to 18 days.

After the second molt the larvae have 12 post-cephalic somites and 11 pairs of legs. In this and all succeeding stadia only the second, third, and fourth somites, and also the seventh somite of males, bear one pair of legs. During the second molt one pair of legs is added to the sixth somite, and two pairs are added to both the seventh and the eighth somites. Fabre (1855), vom Rath (1886), and Latzel (1884) stated that the third instar males of *Polydesmus* spp. have 10 pairs of legs and that the females have 11 pairs. Miley (1927) reported that all of 60 of the third instar larvae of *Euryurus erythropygus* and 10 third instar larvae of *Orthomorpha gracilis* which he examined had 11 pairs of legs. The writer carefully examined 50 larvae of the third stadium of *Orthomorpha gracilis* and found that all of them had 11 pairs of legs. The same larvae were reared to the fourth stadium, and among them were both males and females, which are characterized by having 16 and 17 pairs of legs respectively. The third stadium lasted from 13 to 18 days.

With the third molt the number of post-cephalic somites is increased to 15 and two pairs of legs are added to each of the ninth, tenth, and eleventh somites. In place of the second pair of legs on the seventh somite of the male there are single joints of the rudimentary gonopods. The fourth stadium lasted from 16 to 30 days.

After the fourth molt the larvae have 17 post-cephalic somites and two additional pairs of legs on the twelfth, thirteenth, and fourteenth somites. This stadium lasted from 20 to 38 days.

With the fifth molt the post-cephalic somites are increased to 18 and the legs to 26 in the male and 27 in the female. The four additional pairs of legs

appeared on the fifteenth and sixteenth somites. This stadium lasted from 28 to 46 days.

After the sixth molt the larvae have 19 post-cephalic somites; the males have 28 pairs of legs and females have 29 pairs. The two additional pairs were added to the seventeenth somite. The seventh stadium lasted from 42 to more than 60 days.

The adult number of somites and legs is reached at the seventh and last molt, and the rudimentary male gonopods of the larval stadia are replaced by complete copulatory appendages. The seventh molt adds one somite and two pairs of legs. Five millipedes reared from eggs which were collected in September and October passed through the seven larval stages in 148, 157, 159, 171, and 177 days respectively. Other larvae from the same clutches of eggs were still in the seventh stadium in April, 189 days after they hatched. The sum of the smallest numbers of days during which each of the seven stadia lasted was 132; the sum of the greatest numbers of days was 206 or more. The length of any stadium varied for individuals from the same clutch of eggs reared in the same dish under apparently similar conditions; it was prolonged by subjecting the larvae to a prolonged temperature of 3.5°C. or by allowing the substratum in the culture dishes to become somewhat dry.

It is not definitely known how long adult hothouse millipedes live under ideal conditions. They can be found at all times of the year in greenhouses, but they are never so numerous there as larvae are. Several adult individuals lived more than two months in a laboratory culture; their color at the beginning of that period indicated that they had been in the last stadium at least three weeks. Adults in cultures in the Duke Forest died, but larvae under the same conditions lived throughout the winter. No adults could be found in a locality on the Woman's College campus, Duke University, where many larvae of the latter stadia were collected in February, March, and April; adults were found there in May.

Molting.—The rigid exoskeleton of diplopods prevents growth of the body and must be shed at the end of each stadium. Along with it go the chitinous intima of the fore gut, hind gut, tracheae, and glands; part of the calcium of the exoskeleton is dissolved and absorbed to be used again in the formation of a new exoskeleton; at the same time new internal organs and structures are formed, and a reconstruction, or possibly a complete histolysis, of some of the old organs takes place (Verhoeff 1928, 1937). During part of this complicated process millipedes are completely helpless and immobile, and many pass through it in molting chambers which they prepare.

Orthomorpha gracilis molts seven times; each time a definite number of somites, from one to three, and legs, from two to five pairs, are added. The new somites always appear between the anal somite and the somite last added, and the new legs are added to the somites immediately posterior to the somites already bearing legs. The molting process may be divided into four periods.

During the first, the preparatory period, the larvae hollow out cavities in the

substratum and "plaster" the walls with particles of soil and organic material which they ingest and discharge from the anus. A molting chamber is somewhat flattened, roughly round or elliptical, and about the length of the larva that makes it.

After the completion of the molting chamber the larva enters the period of rigidation. The sternites are pushed far apart so that the integument between them is visible, and the body length is about 15 per cent longer than it is at any other time during that particular stadium. Because of internal pressure the mouth parts protrude, the head bends sharply ventrad, limbs stand out motionless, and the larva lies on its side in a loose semicircle. The color of a larva of one of the later stadia changes during this period from amber to cream tinged with pale red. This loss of color is due to the fact that the old exoskeleton is being dissolved (Verhoeff 1928). If a larva is touched during this period there is no muscular response because a histolysis of the muscles that move the exoskeleton is in progress. Near the end of this period a leg bud appears for each additional leg that the millipede will have after molting. It is possible to see the new somite through the thin, clear exoskeleton that remains.

The intermediate period, when the actual shedding of the skeleton occurs, is shorter than any other phase of the molting process. Internal pressure splits the exoskeleton between the collum and the head and longitudinally along the midventral line. The pressure is the result of the swollen body and of greatly increased respiratory and heart movements; it slowly forces the exuvae off the body dorsally and leaves the larva white, moist, and weak, with the body in a semicircle and the legs and antennae directed caudad.

In the recovery period that follows the only activities seen at first are heart beat and respiratory movements. Soon the larva slowly bends its legs and antennae, and within three or four hours after molting it begins to crawl about inside the molting chamber. It usually devours the exuvae within three or four days, and several days after molting it breaks out of the molting chamber while the exoskeleton is still somewhat soft and conspicuously white or cream colored or firmer and light brown.

The first molt differs from all of the others in that it is the shortest one and it does not take place within a molting chamber, but at the place where the almost immobile larva emerged from the egg. About twelve hours after hatching three pairs of leg buds can be seen on each larva, and six to twelve hours later the thin exoskeleton splits just behind the head and the larva of the second stadium slowly emerges. When the time for the second molt approaches the larvae have become active, crawled away into crevices of the soil, and hollowed out for themselves tiny disk-shaped chambers that are about the length of their curved bodies.

With each succeeding molt the chambers are larger and more carefully constructed and the molting period is longer. In the greenhouses molting larvae of the second through the fifth stadia were found in the greatest numbers in chambers one to two centimeters below the surface in lumps of fine loam.

TABLE 2.—The Percentage of Sixth Instar Larvae of *Orthomorpha gracilis* that Molted within Forty Days under Varied Substrata and Temperature Conditions.

Substratum	29°-31° C.		12°-20° C.		3.5° C.		Summary for Each Substratum	
	No. Larvae	Per-centage Molted	No. Larvae	Per-centage Molted	No. Larvae	Per-centage Molted	No. Larvae	Per-centage Molted
Loam	20	40	30	50	10	0	60	38.3
Sand	10	0	10	30	10	0	30	10.0
Leaf Mold	30	33	20	60	10	0	60	36.6
Summary for each temperature	60	30.0	60	50.0	30	0		

Although active larvae fed largely on manure where there was an opportunity, they were rarely found in molting chambers in manure. Molting larvae of the sixth and seventh stadia were observed at depths of from three to eight centimeters in loose soil. In the laboratory molting was easily observed if the larvae were placed in flasks or fingerbowls which contained a layer of soil from one-half to two centimeters in depth. Under such conditions the larvae often constructed their molting chambers on the bottom of the containers and the molting process could be seen through the glass. At no time were the molting chambers of the hothouse millipede found on top of the soil where some other polydesmid millipedes construct theirs.

The molting process between the fifth and sixth stadia lasted ten days, of which the preparatory period was two days, the rigidation period four days, the intermediate period about six hours, and the recovery period four days. The molting process between the sixth and seventh stadia lasted 14 days; between the seventh and eighth stadia it lasted about 20 days. If the molting chamber were destroyed early in the preparatory period the larva constructed another. The molting chambers of a larva of the seventh stadium were destroyed three times; finally the larva passes into the rigidation period on the surface of the soil.

There was no difference noted between the time required for larvae to molt in the warm air chamber and in the laboratory. Larvae on a substratum of sand did not construct molting chambers at any of the temperatures tried, nor did they in loam or in leafmold at a temperature of 3.5°C.

The percentages of sixth instar larvae that molted within 40 days when on a substratum of leafmold, loam, or sand and at temperatures of 3.5°, 12°-20°, or 29°-31°C. are given in Table 2. None of the 25 larvae of this stadium that were in outdoor cultures in the Duke Forest between October and March molted.

Food Habits

McDaniel (1931) reported that *Orthomorpha gracilis* is a serious problem in forcing houses because it eats tender shoots and roots of plants. Specimens were received from Sanford, North Carolina, where they were reported to be

injurious to trees. Workers in greenhouses in Durham, North Carolina, said that they did not believe that the hothouse millipede injures their plants.

In laboratory experiments *Orthomorpha gracilis* ate no living plant tissues. Larvae of the sixth stadium and adults at laboratory temperatures did not eat fresh lettuce or sprouting beans; their loss of weight during a period of 12 days when those two plants were offered as food was as great as that lost by control millipedes under similar conditions but without fresh lettuce or sprouting beans.

The weight of the feces from larvae of the seventh stadia and adults living on loam, leafmold, or manure and subjected to two ranges of temperature are given in Table 3. All of the millipedes used in this experiment were taken from the same stock cultures in the laboratory. No feces were produced when the animals were kept at a temperature of 3.5°C. None ate the fruiting bodies of basidiomycetes or moist, decayed wood at laboratory temperatures. They sometimes ate wet filter paper when loam, manure, or leafmold was available.

TABLE 3.—The Percentage of Body Weight of Feces from Ten Seventh Instar Larvae and Ten Adults of *Orthomorpha gracilis* that Fed Twenty-four Hours on Manure, Loam, and Leafmold under Temperatures from 29° to 31° C. and from 12° to 20° C.

Food	Seventh Instar Larvae		Adult Millipedes		Mean Percentage of Weight of Feces
	29°-31° C.	12°-20° C.	29°-31° C.	12°-20° C.	
Manure	55.2	97.5	64.4	27.3	60.7
Leafmold	131.2	48.2	38.7	43.1	65.4
Loam	92.4	12.6	39.1	37.9	45.5
Mean Percentage of Weight of Feces.....	92.9	52.8	47.4	36.1	

Toleration to Variations in Humidity, High and Low Temperatures, and Submersion in Water

At laboratory temperatures hothouse millipedes died within 15 hours after they were put into jars in which the relative humidity values were 0 and 14 per cent; at humidity values of 32 and 65 they died within 20 hours; at humidity values of 51 and 76 per cent they died within 23 hours; at 90 per cent they died within 30 hours; and at 100 per cent they lived until death resulted from starvation. In all cases death occurred when the water lost was between 40 and 45 per cent of the total water content of the body. When the millipedes were subjected to increased temperatures under relative humidity values between 0 and 100 per cent they died at a temperature between 39° and 39.5°C. This experiment was carried on too rapidly for any correlation between the lethal temperature and relative humidity to be noted.

Of 30 larvae of the sixth stadia that were subjected to a temperature of 3.5°C., 13 were alive after four months. At this temperature they remained motionless, but if taken into a warm room they began moving and eating within

15 minutes. When these larvae and larvae from cultures in the laboratory were subjected to temperatures just low enough to freeze them quickly, they all recovered; if frozen 30 minutes or longer, larvae from neither group survived. Adult millipedes reacted similarly to freezing temperatures.

Orthomorpha gracilis adults lived from five to seven days when submerged in water. There was considerable wriggling during the first 10 to 12 hours; following that there was little movement except when they were removed from the water. The body increased 20 per cent in length after five days in water.

Summary

1. *Orthomorpha gracilis*, a polydesmid millipede with wide distribution throughout the tropical and temperate regions of the world, occurs in greenhouses in the United States and in the open in southern states.

2. The adults are known to breed throughout the year in a greenhouse where a temperature above 22°C. is maintained. Eggs are deposited in clutches of from 300 to 17. The incubation period of the eggs at heated room temperatures is approximately ten days.

3. The seven larval stadia can be distinguished by differences in body size and numbers of post-cephalic somites and pairs of legs. Females of all stadia from the fourth through the eighth are larger and have one more pair of legs than the males. The duration of each stadium increases successively from the first, which lasts approximately 24 hours, through the seventh, which lasts 60 or more days at heated room temperatures, and the eighth, which is known to last more than two months. Five specimens passed through the seven larval stadia in from 148 to 177 days at heated room temperatures. At lowest temperatures the length of the larval periods is increased.

4. Larvae pass from one stadium to the next by anamorphic molts, of which the second through the seventh take place in molting chambers constructed in the soil by the larvae. The time required for molting at heated room temperatures increases with each succeeding molt from three to six hours for the first molt to 20 days for the seventh. During the fourth molt the preparatory period lasts two days, the rigidation period four days, the actual molting six hours, and the recovery period four days.

4. No evidence was found that either larvae or adults eat living plant tissues. At heated room temperatures the ingestion of soil and organic matter, as determined by collecting and weighing feces, was 48.9 per cent greater by seventh instar larvae than by adult millipedes. At a temperature range of 12°C.-20°C. the consumption of the seventh instar larvae was 31.6 per cent greater than that of the adults.

5. The high lethal temperature is between 39°C. and 39.5°C. at relative humidities between 0 and 100 when the increase in temperature is at the rate of one degree centigrade in five minutes. Quick freezing temperatures over a period of thirty minutes are fatal. Adults and larvae of the seventh stadium died within 30 hours at humidities of 90 per cent or less; at 100 per cent they lived several days. Adults survived submersion in water from five to seven days.

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Studies in the Nearctic Freshwater Amphipoda, III

Notes on the Freshwater Amphipoda of Eastern United States,
with Descriptions of Ten New Species

Leslie Hubricht

Descriptions of most of the older species of freshwater Amphipoda of the eastern United States being inadequate, it was essential that material from the type localities be examined in order to fully understand the species. As such material was not available, the author undertook to make collections at as many of these type localities as could be located. As a result, most of the species were obtained at the type localities, or so near as to leave little doubt as to the determinations. In addition, in the regions traversed, a large number of collections were made which add to our knowledge of the distribution of these species. This paper is a report on these collections, together with some material collected by other persons and examined by the author.

The author was aided by a Research Grant from the American Association for the Advancement of Science. He is also indebted to the owners of the caves visited for permission to collect in their caves and for many courtesies.

Family TALITRIDAE

Genus HYALELLA S. I. Smith

1874. *Hyaella* S. I. Smith, Rept. U. S. Fish. Comm. 22:645.

HYALELLA AZTECA (Saussure)

1858. *Amphiloë aztecus* Saussure, Mém. Soc. Phys. Hist. Nat. Genève 14:474, pl. 5, fig. 33.

1888. *Hyaella azteca* (Saussure). Stebbing, Rept. Voy. Challenger 29:311.

1907. *Hyaella knickerbockeri* (Bate). Weckel, Proc. U. S. Nat. Mus. 32:54, fig. 15.

Localities.—PENNSYLVANIA: CHESTER Co. spring, 1 mile west of Exton. CENTRE Co.: Spring Creek, Lemont. VIRGINIA: WASHINGTON Co.: large spring, 2 miles east of Wallace. WEST VIRGINIA: POCAHONTAS Co.: spring, Huntersville. GEORGIA: CHATTOGA Co.: spring, Summerville. FLORIDA: SUWANNEE Co.: large spring, Branford; Ichucknee River, 2 miles east of Hildreth. JACKSON Co.: tupelo swamp, 7 miles east-southeast of Marianna. ALABAMA: FAYETTE Co.: slough, 0.8 mile east of Fayette. BIBB Co.: slough of Haysop Creek, 1 mile southwest of Brent. MICHIGAN: WASHTENAW Co.: pond, just south of Ypsilanti Airport, 5 miles southeast of Ann Arbor. LENAWEE Co.: pond, 2 miles northwest of Hudson; pond 0.7 miles southwest of Addison. INDIANA: HUNTINGTON Co.: slough, 3.3 miles northeast of Huntington. GRANT Co.: stream, 0.4 miles northwest of Mathews. LAKE Co.: creek, 2 miles north of Hobart. LAPORTE Co.: Lily Lake, 0.5 mile north of LaPorte. ILLINOIS: COOK Co.: Tuma Slough, Palos Hills. MISSOURI: DENT Co.: Montauk Spring, Montauk. TEXAS: REAL Co.: spring, head of Camp Wood Creek, 8 miles south of Camp Wood.

Genus ORCHESTIA Leach

1814. *Orchestia* Leach, Edinb. Enc. 7:402.

ORCHESTIA UHLERI Shoemaker

1930. *Orchestia uhleri* Shoemaker, Jour. Wash. Acad. Sci. 20:108.

Localities.—SOUTH CAROLINA: COLLETON Co.: tidal marsh, 6 miles southwest of Green Pond. FLORIDA: PUTNAM Co.: among Water-Hyacinths, along St. Johns River, opposite Palatka. SEMINOLE Co.: marsh, near Lake Monroe, 2.2 miles northwest of Sanford.

Family GAMMARIDAE

Genus GAMMARUS Fabricius

1775. *Gammarus* (part), J. C. Fabricius, Syst. Ent., p. 418.

GAMMARUS TROGLOPHILUS Hubricht & Mackin

1940. *Gammarus troglophilus* Hubricht & Mackin, Amer. Midl. Nat. 23:189, fig. 1.

Localities.—ILLINOIS: GREENE Co.: spring at base of bluff, 3 miles north of Eldred. JACKSON Co.: small spring near north end of Horseshoe Bluff, 5 miles northwest of Pomona. MONROE Co.: stream in Ice Cave, Camp Vandeventer, 5 miles west of Waterloo. MISSOURI: MARION Co.: spring, 4 miles north of Palmyra. RALLS Co.: spring, 7 miles south-southeast of New London. PIKE Co.: small spring, 4 miles south of Clarks-ville. LINCOLN Co.: cave spring, 2.5 miles south of Winfield; small spring, 1.5 miles north of Old Monroe. STE. GENEVIEVE Co.: stream in Gillam Cave, 5 miles south of Ste. Genevieve; stream in Kolm Cave, 2.5 miles southwest of Ste. Genevieve. PERRY Co.: stream in Schindler Cave, 3 miles east-northeast of Perryville; pools, Steffens Cave, near Crosstown; stream in small cave, 1.2 miles southwest of Menfro; stream in Mecker Cave, 3 miles west-northwest of Longtown.

GAMMARUS LIMNAEUS S. I. Smith

1874. *Gammarus limnaeus* S. I. Smith, Rept. U. S. Fish. Comm. 2:651, pl. 2, figs. 6-7.

LOCALITIES.—MICHIGAN: JACKSON Co.: spring, just west of Concord. CALHOUN Co.: stream, 3.3 miles east of Burlington. BRANCH Co.: stream, 5 miles west of Union City. ILLINOIS: COOK Co.: stream, Black Partridge Woods, 1.5 miles northwest of Lemont. WILL Co.: Buffalo Creek, 0.6 miles northeast of Plainfield. FULTON Co.: outlet of drain, 1.4 miles south of Avon. PEORIA Co.: spring, 3.1 miles west of Princeville. PUTNAM Co.: spring, 3.2 miles north of Putnam. PIKE Co.: small spring, 1 mile southeast of Pearl. JACKSON Co.: spring, Happy Hollow, Fountain Bluff, 2.3 miles south of Gorham; small spring near north end of Horseshoe Bluff, 5 miles northwest of Pomona; small intermittent stream, Little Grand Canyon, 5 miles west of Etherton. UNION Co.: spring, 1 mile northeast of Larue; spring, 2 miles east of Reynoldsville; stream in Wet Cave, near Roaring Spring, 6 miles south of Anna; Roaring Spring, 6 miles south of Anna. HARDIN Co.: Cave Spring, 2.3 miles south of Eichorn. MISSOURI: MARION Co.: spring, 4 miles north of Palmyra. RALLS Co.: stream in Fisher Cave, 5 miles south-southeast of New London; spring, 7 miles south-southeast of New London. PIKE Co.: inlet of cave, 0.2 mile north of Frankford. ST. CHARLES Co.: spring, Weldon Springs; small spring, 1.3 miles northwest of Augusta. STE. GENEVIEVE Co.: stream in small sandstone cave, 3.6 miles southeast of Bloomsdale. ST. FRANCOIS Co.: stream in Shaver Cave, 1.5 miles north of Bonne Terre; small spring, 2 miles north-northeast of Bismarck. IRON Co.: creek, Peters Cave Hollow, 9 miles southwest of Banner. REYNOLDS Co.: small spring, near Reeds Spring, east of Centerville. WARREN Co.: small spring, at the Big Rock, 1.6 miles northwest of Case. WASHINGTON Co.: small spring, 2 miles west of Fertile; Crystal Spring, Old Mines. PULASKI Co.: small spring, near Ash Cave, 2.5 miles west of Jerome; Hancock Spring, 2 miles east of Crocker. BOONE Co.: stream in Hunters Cave, 5 miles north-northwest of Ashland. OSAGE Co.: stream in Dowlers Cave, 3 miles west of Cooper Hill; spring, Cooper Hill.

MILLER Co.: small spring, below Klugs Cave, 2.4 miles south of Marys Home. ARKANSAS: LAWRENCE Co.: Wautuga Springs, 2.9 miles southeast of Ravenden (Horton H. Hobbs, coll.). OKLAHOMA: WOODS Co.: Bat Cave Spring, 4 miles northeast of Freedom.

GAMMARUS MINUS Say

1818. *Gammarus minus* Say, Jour. Acad. Nat. Sci. Phila. 1:373.

1902. *Gammarus propinquus* W. P. Hay, Proc. U. S. Nat. Mus. 25:224.

Localities.—PENNSYLVANIA: CHESTER Co.: spring, 1 mile west of Exton. LANCASTER Co.: spring, 4 miles west of Paradise. MIFFLIN Co.: stream in Alexander's Cavern, Naginety. HUNTINGDON Co.: spring, 8 miles southwest of Pine Grove Mill. BLAIR Co.: stream in Arch Spring Cave, 7.5 miles southwest of Water Street. BEDFORD Co.: spring, northwest of Maria. WEST VIRGINIA: GRANT Co.: large spring, 1 mile east of Cabins. PENDLETON Co.: small spring, 0.4 mile south of Cherry Grove. RANDOLPH Co.: stream in Gandy Creek Sink Cave, Osceola. GREENBRIER Co.: stream in Higginbotham Cave, 1.5 miles southwest of Frankford; stream in Organ Cave, near Organ Cave P. O. VIRGINIA: BOTETOURT Co.: Oak Spring, 8.3 miles north-northeast of Buchanan. PULASKI Co.: spring, 4.5 miles south-southwest of Pulaski. TAZEWELL Co.: Maiden Spring, 3.5 miles southwest of Liberty Hill; stream, Lost Mill Sink, Liberty Hill. WASHINGTON Co.: spring, 1.5 miles southwest of Glade Springs. INDIANA: LAWRENCE Co.: stream, Twin Caves Sink, and Lower Twin Cave, Spring Mill State Park. CRAWFORD Co.: Sharp's Spring, Wyandotte. MARTIN Co.: spring, 2 miles northeast of Dover Hill; Ellis Spring, 3.5 miles east of Loogootee. KENTUCKY: WOODFORD Co.: small spring, 3 miles north of Versailles. TENNESSEE: MARION Co.: mouth of Nickajack Cave, Shellmound. DE KALB Co.: stream in Ted Cave, 5 miles east of Smithville. SUMNER Co.: spring, 2.8 miles south of Westmoreland. ALABAMA: JACKSON Co.: Blowing Cave Spring, 8.5 miles southwest of Scottsboro. MISSOURI: ST. CHARLES Co.: spring, 2.3 miles south of Howell. STE. GENEVIEVE Co.: Vallee Spring, 1 mile south of Ste. Genevieve. WASHINGTON Co.: spring, near Hamilton Cave, 5.5 miles southeast of Sullivan. SHANNON Co.: Welch Spring, 1 mile northwest of Akers; Medlock Cave Spring, 2 miles northwest of Akers. CARTER Co.: Big Spring, 4 miles south of Van Buren. PULASKI Co.: spring, near Piquet Cave, 4 miles southwest of Dixon. STONE Co.: Woods Spring (G. K. Noble, coll.). NEWTON Co.: spring, 2.7 miles northeast of Neosho; spring, 1.4 miles north of Tipton Ford; Big Spring, Neosho. ARKANSAS: SEARCY Co.: spring, mouth of Great Hurricane Cave. NEWTON Co.: Big Spring, Bella Vista; spring, 2 miles south of Gentry. OKLAHOMA: MAYES Co.: spring at roadside park, 1 mile east of Locust Grove.

Remarks.—There are three varieties of this species. One found in springs, is brown with large well developed eyes, and short antennae. The other two are found in caves and are bluish in color. Of these, the commoner form has slightly reduced eyes and long antennae. The other form has been found only in Greenbrier Co., West Virginia. In it the eyes are greatly reduced, the antennae are long, the gnathopoda and peraeopoda are more slender, and the entire body is more fragile. It probably represents a very old immigration into the caves. It has been named variety *tenuipes* by Shoemaker.

Arch Spring Cave in Pennsylvania, Gandy Creek Sink Cave in West Virginia, and Ted Cave in Tennessee are tunnels with a stream running in one end and out the other. Here this species is found only in the total darkness of the caves and does not occur in the streams before they enter, or after they leave the caves. At Twin Caves, Indiana, a stream flows from one cave for about 100 feet and then enters another. In the lighted region the spring variety of the species is found. In the total darkness of the lower cave the cave form

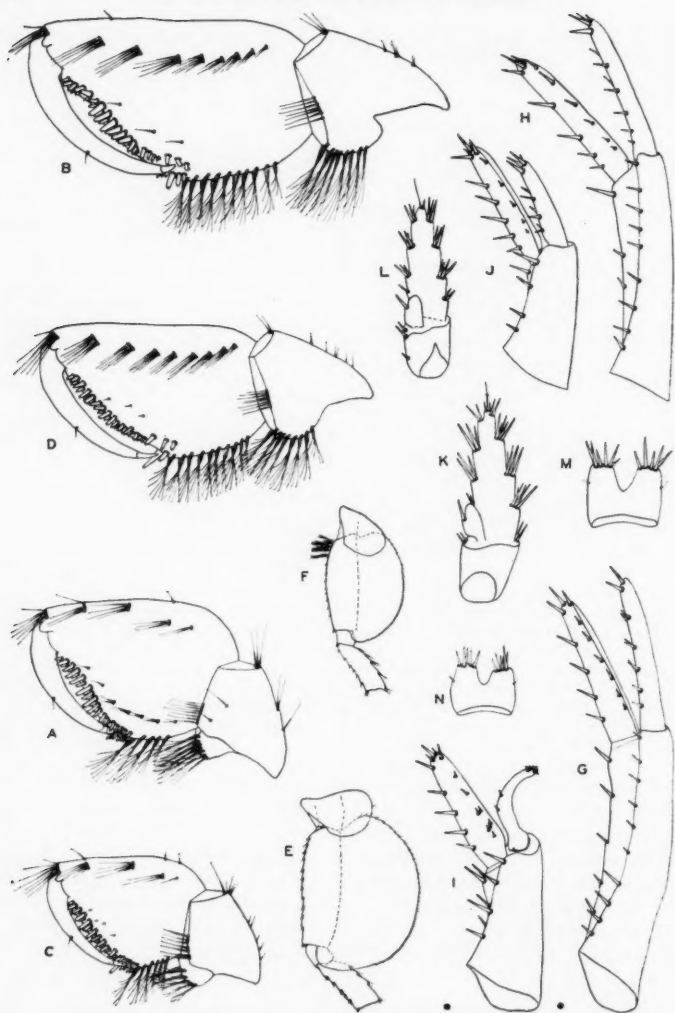


PLATE 1. *Crangonyx anomalus*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first three segments of fifth pereopod, male; F, first three segments of fifth pereopod, female; G, first uropod, male; H, first uropod, female; I, second uropod, male; J, second uropod, female; K, third uropod, male; L, third uropod, female; M, telson, male; N, telson, female.

occurs, and in the twilight zone neither is found. At Nickajack Cave, Tennessee, Blowing Cave, Alabama, and at many of the Ozark caves in Missouri they occur in the stream at the mouths of the caves but not in the caves themselves.

From the above data it can be seen that there is no close relationship between the epigean and the subterranean forms. The individuals adapted to each habitat tend to remain there and that it is only rarely an individual moves from one habitat to another.

GAMMARUS FASCIATUS Say

1818. *Gammarus fasciatus* Say, Jour. Acad. Nat. Sci. Phila. 1:372.

Localities.—SOUTH CAROLINA: COLLETON Co.: tidal marsh, 6 miles southwest of Green Pond. FLORIDA: SEMINOLE Co.: Lake Monroe, 2.2 miles northwest of Sanford. SUWANEE Co.: Ichlucknee River, 2 miles east of Hildreth. WAKULLA Co.: Wakulla River, 2.5 miles southwest of Wakulla.

Genus ALLOCRANGONYX Schellenberg

1936. *Allocrangonyx* Schellenberg, Mitt. Zool. Mus. Berlin 22(1):33.

ALLOCRANGONYX PELLUCIDUS (Mackin)

1935. *Niphargus pellucidus* Mackin, Trans. Amer. Micro. Soc. 54:42, pl. 11.

1936. *Allocrangonyx pellucidus* (Mackin). Schellenberg, Mitt. Zool. Mus. Berlin 22(1):33.

Localities.—MISSOURI: PHELPS Co.: stream in Saltpetre Cave, 7 miles north of Newburg. PULASKI Co.: stream in Maxey Cave, 1.5 miles north of Hanna. OKLAHOMA: MURRAY Co.: seep, 0.4 mile northwest of Turner Falls, Arbuckle Mts.

Remarks.—The development of the outer ramus of the third uropod in this species is remarkable. The young have one large basal segment and a small terminal one. This terminal segment is later absorbed so that in half-grown specimens the ramus is composed of but a single segment. As the males reach maturity the basal segment elongates and divides until there may be as many as twelve segments. Mature females have only one segment.

This species was described from depauperate or immature specimens. Well developed specimens may reach a body length of 25 mm.

Genus CRANGONYX Bate

1859. *Crangonyx* Bate, Proc. Dublin Univ. Zool. Bot. Assoc. 1:237.

1899. *Eucrangonyx* Stebbing, Trans. Linn. Soc. London II, 7:423.

Crangonyx anomalus, sp. nov.

Plate I

Description.—Males reach a length of 22 mm., females 19 mm., exclusive of appendages. Color in life very pale lavender-gray. Eyes small, round.

All figures were made with the aid of a camera lucida. The distance between the two dots on the lower margin of each plate represents one millimeter (peraeopod figures when shown are not to scale). All gnathopod figures are inside view.

First antenna about one-half as long as the body, with up to thirty-two articles in the flagellum of the male and twenty-eight in the female. Second antenna three-fifths as long as the first, with up to twelve articles in the flagellum of the male and ten in the female. Second antenna of the mature male armed with thirteen small paddle-shaped sensory organs; four on the fourth segment of the peduncle, five on the fifth segment, and one each on the first four segments of the flagellum.

Palmar margins of the propodi of the gnathopoda of the male concave, curving gradually into the posterior margin, and armed with twenty-five to thirty-five notched spines of unequal size on each side. Superior lateral setae in short transverse rows of two to six. Inferior lateral setae very small, solitary or in pairs. Setae on the posterior margin of the propodus in transverse rows on both gnathopoda. Gnathopoda of the female similar to those of the male but the palmar margins not as strongly concave.

Second segments of the third, fourth and fifth pereopoda greatly expanded posteriorly and finely serrate.

Outer ramus of the first uropod only slightly shorter than the inner ramus. The second uropod with the outer ramus about two-thirds as long as the inner ramus, straight in the female, cylindrical, curved outward, and with about six small, curved spines on the tip and two small lateral spines in the male. Outer ramus of the third uropod a little more than twice the length of the peduncle and armed on each side with three or four fascicles of spines.

Telson broader than long, cleft about one-half the distance to the base. Each lobe armed with about six spines.

C. anomalus differs from all other species of the genus in that the males are larger than the females, and in the greatly expanded and finely serrate second segments of the third, fourth, and fifth pereopoda. The sensory organs on the second antenna of the male are smaller than in any other species. It is probably most closely related to *C. forbesi*.

Cotypes.—Spring along Bryan Station road, 0.3 mile northeast of Eastin Road, 3 miles northeast of Lexington, Fayette Co., Kentucky. U. S. Nat. Mus. cat. no. 79329; and collection of the author. A U. S. topographical map, Lexington, Ky., quadrangle, with the locations of the type localities of this species and *Synurella dentata* marked upon it has been deposited at the U. S. National Museum acc. no. 158/208.

Localities.—OHIO: CLINTON Co.: small spring, 0.7 mile southeast of Westboro. GREENE Co.: spring, John Bryan State Park, 2 miles west of Clifton. BROWN Co.: spring, 5 miles south of Georgetown; spring rill, 1.8 miles south of Georgetown. KENTUCKY: MASON Co.: spring, 1.6 miles north of Washington. BOURBON Co.: small spring, 2.8 miles southwest of Millersburg; spring, 5.7 miles southwest of Paris. FAYETTE Co.: spring along Bryan Station Road, 0.3 mile northeast of Eastin Road, 3 miles northeast of Lexington. GARRARD Co.: springs, 2 miles northwest of Lancaster.

This species is apparently restricted to springs issuing from the Ordovician limestones of the Cincinnati anticline.

CRANGONYX OBLIQUUS (Hubricht & Mackin)

1940. *Eucrangonyx obliquus* Hubricht and Mackin, Amer. Midl. Nat. 23:195, fig. 4.
1940. *Crangonyx richmondensis* Ellis, Charleston Mus. Leaf. 13:3, 2 figs.

Localities.—SOUTH CAROLINA: BERKELEY Co.: slough, 3 miles northwest of Cordesville. JASPER Co.: slough, 2 miles south-southwest of Ridgeland. GEORGIA: WAYNE Co.: swamp, 1.1 miles northeast of Jesup. OHIO: PREBLE Co.: outlet of drain, 0.2 miles northwest of New Hope. MICHIGAN: WASHTENAW Co.: pond, just south of the Ypsilanti Airport, 5 miles southeast of Ann Arbor; pond on Platt Road, 0.5 miles north of Bemis Road. INDIANA: HANCOCK Co.: ditch, 3.3 miles east of Greenfield. PUTNAM Co.: Triple Springs, near Pleasant Gardens. HENDRICKS Co.: temporary spring, 4 miles southwest of Belleville. WAYNE Co.: small spring, about 8 miles west of Economy. ORANGE Co.: spring, 8.6 miles south of Paoli. MARTIN Co.: Ellis Spring, 3.5 miles east of Loogootee. KENTUCKY: BUTLER Co.: Jeff Taylor Spring, 1 mile south-southwest of Martin Ferry (Borah). CHRISTIAN Co.: spring, Pollard farm, 16.5 miles northwest of Hopkinsville. TENNESSEE: DAVIDSON Co.: spring, "Fortland," near Shelby Park, Nashville. ALABAMA: JACKSON Co.: slough, 1.6 miles northwest of Paint Rock. MADISON Co.: slough, 2.7 miles northwest of Gurley. MISSISSIPPI: RANKIN Co.: slough, 0.8 miles west of Pelahatchee. ILLINOIS: CHAMPAIGN Co.: ditch, Savoy (H. J. Van Cleave, coll.). EFFINGHAM Co.: ditch, 1.9 miles west-southwest of Altamont; temporary stream, 1 mile south-southwest of Funkhouser. MADISON Co.: spring, 0.4 miles southwest of Troy. MISSOURI: BUTLER Co.: slough, 6.1 miles of Neelyville. ARKANSAS: PHILLIPS Co.: temporary pool, 5.5 miles north of Barton. MONROE Co.: stream, 4.5 miles southwest of Clarendon; slough, 1.1 miles north of Holly Grove. JEFFERSON Co.: slough 4.3 miles northeast of Altheimer. PERRY Co.: cypress swamp, 2 miles north of Perry. FAULKNER Co.: temporary stream, 0.6 miles south of Wooster. YELL Co.: temporary pool, 0.4 mile west of Danville. LOUISIANA: LINCOLN Co.: slough, 0.9 miles south of Dubach.

CRANGONYX SERRATUS (Embody)

1910. *Eucrangonyx serratus* Embody, Proc. U. S. Nat. Mus. 38:299.
1936. *Crangonyx serratus* (Embody). Schellenberg, Mitt. Zool. Mus. Berlin. 22:35.

Locality.—FLORIDA: JEFFERSON Co.: 5.8 miles east of Capps (Horton H. Hobbs, coll.).

CRANGONYX FORBESI (Hubricht & Mackin)

1940. *Eucrangonyx forbesi* Hubricht & Mackin, Amer. Midl. Nat. 23:196, fig. 5.

Localities.—ILLINOIS: JACKSON Co.: small intermittent stream, Little Grand Canyon, 5 miles west of Etherton; spring, Happy Hollow, Fountain Bluff, 2.3 miles south of Gorham. UNION Co.: spring, 2 miles east of Reynoldsville. MISSOURI: MARION Co.: spring, 4 miles north of Palmyra. RALLS Co.: stream in Fisher Cave, 5 miles south-southeast of New London. PIKE Co.: stream in cave, 0.2 mile north of Frankford. LINCOLN Co.: Cave Spring, 2.5 miles south of Winfield. ST. CHARLES Co.: spring, Weldon Springs. STE. GENEVIEVE Co.: spring, south side of Beckett Hills; spring, Zell; stream in Kolms Cave, 2.5 miles southwest of Ste. Genevieve; stream in Gillam Cave, 5 miles south of Ste. Genevieve. PERRY Co.: stream in Schindler Cave, 3 miles east-northeast of Perryville; pools, Steffens Cave, near Crosstown. WARREN Co.: small spring, at the Big Rock, 1.6 miles northeast of Case. WASHINGTON Co.: stream in Hamilton Cave, 5.5 miles southeast of Sullivan; stream in Greens Cave, 4.5 miles south-east of Sullivan. IRON Co.: small spring, 2 miles north of Bellevue. ST. FRANCOIS Co.: small spring, 1.5 miles northeast of Doe Run. OREGON Co.: Greer Spring, 1.3 miles north of Greer. MADISON Co.: spring, 0.5 miles south of Mill Creek. MARIES Co.: stream in Boulware Cave, 12 miles south of Vienna. PHELPS Co.: stream in Gourd Creek Cave, 2 miles east of Vessie. PULASKI Co.: stream, mouth of Maxey Cave, 1.5 miles north of Hanna; stream in Ash Cave, 2.5 miles west of Jerome; stream in Spring Cave, 5 miles south of Crocker; stream in Wind Cave, 5 miles south of Crocker; stream, mouth of Picket Cave, 4 miles southwest of Dixon; stream in Grep Cave, 1.3

miles north of Franks; Miller Spring, 3 miles northeast of Big Piney. SHANNON Co.: stream, Cave Hollow Cave, near Ebb and Flow Spring, 6 miles north of Montier; spring, near Jacks Fork, north of Teresita. TEXAS Co.: spring, mouth of Bat Cave, 7 miles northeast of Success. MILLER Co.: small stream, in small cave, 0.3 miles southeast of Miller County Home, 3 miles southeast of Tuscumbia; stream in Barnett Cave, 3.3 miles south of Iberia. LACLEDE Co.: spring, mouth of Davis Cave, 1.4 miles south of Pease; small stream, near Bennett Spring; spring, 2.4 miles west of Hazelgreen. DALLAS Co.: springs, 4.2, 3.7, and 0.6 miles east of Louisburg. HICKORY Co.: small stream, 4 miles northeast of Weaubleau. ST. CLAIR Co.: spring, Collins. JASPER Co.: Dowler Spring, Sarcosie. CHRISTIAN Co.: stream in Smallin Cave, 2.8 miles northeast of Ozark. ARKANSAS: LAWRENCE Co.: spring, 3.7 miles south of Imboden. OKLAHOMA: MAYES Co.: spring at roadside park, 1 mile east of Locust Grove.

CRANGONYX HOBBSI Shoemaker

1941. *Crangonyx hobbsi* Shoemaker, Charleston Mus. Leaf. no. 16, p. 9, 2 figs.

Locality.—FLORIDA: LEVY Co.: from driven well 50 feet deep, 1.5 miles northeast of Chiefland (A. Hyatt Verrill, coll.).

CRANGONYX ANTENNATUS Packard

1881. *Crangonyx antennatus* Packard, Amer. Nat. 15:880.

1899. *Eucrangonyx antennatus* (Packard). Stebbing, Trans. Linn. Soc. London II, 7:423.

1902. *Niphargus antennatus* (Packard). W. P. Hay, Proc. U. S. Nat. Mus. 25:429.

Localities.—VIRGINIA: LEE Co.: stream in Cudjo's Cave, near Cumberland Gap. TENNESSEE: MARION Co.: stream in Nickajack Cave, Shellmound. GEORGIA: FLOYD Co.: pools in Cave Spring Cave, Cave Spring. ALABAMA: JACKSON Co. stream in Blowing Cave, 8.5 miles southwest of Scottsboro. DE KALB Co.: stream in Manitou Cave, 1 mile south of Ft. Payne.

CRANGONYX SHOEMAKERI (Hubricht & Mackin)

1871. *Eucrangonyx shoemakeri* Hubricht & Mackin, Amer. Midl. Nat. 23:198, fig. 6.

Localities.—OHIO: WILLIAMS Co.: temporary pool, 2 miles north of Hamer; temporary pools, 2 miles southwest of Bryan. WOOD Co.: outlet of drain, 1.3 miles southwest of Perryville. SENECA Co.: outlet of drain, 1 mile east of Frank. CLINTON Co.: small spring, 0.7 miles southeast of Westboro. CRAWFORD Co.: outlet of drain, 5 miles south-southwest of Chatfield. CLARK Co.: small stream, 1.3 miles east of Donnellsville. MICHIGAN: GENESEE Co.: outlet of drain, 5.6 miles north of Fenton. MONROE Co.: outlet of drain, 2.8 miles north of Petersham; outlet of drain, 0.5 miles north of Ottawa Lake. BRANCH Co.: ditch, 3.1 miles south of Coldwater. LENAWEE Co.: slough, 0.5 miles west of Hudson. CALHOUN Co.: stream, 3.3 miles east of Burlington. INDIANA: NOBLE Co.: outlet of drain, 0.6 mile southeast of Kendallville. DEKALB Co.: outlet of drain, 5.7 miles east of Corunna. HENRY Co.: outlet of drain, 1.4 miles west of Straughn; outlet of drain, 3.5 miles west of Knightstown; small stream, 1.3 miles northwest of Blountsville. HUNTINGTON Co.: slough, 3.3 miles northeast of Huntington. GRANT Co.: temporary pools, 5 miles west of Jonesboro. PUTNAM Co.: temporary stream, 5.3 miles east-northeast of Harmony. HENDRICKS Co.: spring (temporary?), 2.8 miles east-northeast of Plainfield. KENTUCKY: BOURBON Co.: small spring, 2.8 miles southwest of Millersburg; spring, 5.7 miles southwest of Paris. FAYETTE Co.: spring, along Bryan Station Road, 0.3 mile northeast of Eastin Road, 3 miles northeast of Lexington; spring, 0.8 mile east of Fort Spring; Russell Cave Spring, 7 miles northeast of Lexington; small spring, 2.9 miles south-southwest of Jimtown. JESSAMINE Co.: spring, 6.1 miles north of Nicholasville; spring, 2.7 miles north of Nicholasville. WOODFORD Co.: Sunnyside Farm spring, 4.5 miles east of Versailles. FRANKLIN Co.: small spring, just east of Bridgeport. ILLINOIS: PEORIA Co.: spring, 3.1 miles west of Princeville. KNOX Co.: outlet of drain, 1.6 miles southwest of Galesburg; outlet of drain,

2 miles north of Abington. McDONOUGH Co.: outlet of drain, 3 miles south of Colmar; outlet of drain, 2 miles east of Good Hope. CLARK Co.: spring, 1.9 miles east-northeast of Marshall. CUMBERLAND Co.: ditch, 3.6 miles east-northeast of Greenup. EFFINGHAM Co.: temporary stream, 1 mile southwest of Funkhouser; ditch, 1.9 miles west-southwest of Altamont. BOND Co.: temporary stream, 0.5 mile west of Beavercreek. HENDERSON Co.: outlet of drain, 1.7 miles west of Biggsville. MADISON Co.: spring, 0.4 mile southwest of Troy; temporary pool, near Silver Creek, 3.6 miles west of St. Jacob. UNION Co.: small spring-fed marsh, 2.5 miles east of Ware. IOWA: WASHINGTON Co.: outlet of drain, 1 mile south of Haskins; slough of English River, 2.5 miles east of Riverside. DES MOINES Co.: outlet of drain, 0.2 miles northwest of Danville; outlet of drain, 3.6 miles east of Middletown. MISSOURI: LINCOLN Co.: marsh, 2 miles south of Apex. St. CHARLES Co.: temporary pool, 0.3 mile south of St. Peters.

CRANGONYX GRACILIS GRACILIS S. I. Smith

1871. *Crangonyx gracilis* S. I. Smith, Amer. Jour. Sci. III, 2:453.

1899. *Eucrangonyx gracilis* (S. I. Smith). Stebbing, Trans. Linn. Soc. London II, 7:423.

Localities.—PENNSYLVANIA: Chester. SOUTH CAROLINA: Jasper, Berkeley, Orangeburg. GEORGIA: Chatham, Cobb, Wayne. FLORIDA: Alachua, Seminole, Leon, Jackson. OHIO: Williams. MICHIGAN: Washtenaw, Lenawee, Calhoun. INDIANA: Huntington, Lake, Laporte. KENTUCKY: Laurel, Fayette, Hardin, Jessamine, Bourbon, Lincoln, Garrard. TENNESSEE: Davidson, Bedford, Williamson, Trousdale, Cheatham, Maury, Wilson, Monroe. ALABAMA: Bibb, Jackson, Lawrence, Sumter, Perry, Fayette, Madison, Houston, Talladega. MISSISSIPPI: Rankin, Scott, Newton. ILLINOIS: LaSalle, Cook, Union. MISSOURI: Lincoln, Greene, Butler. ARKANSAS: Union, Calhoun, Arkansas, Dallas, Jefferson, Phillips, Cross, Monroe, Lawrence, Perry, Faulkner, Conway, Yell, Saline. LOUISIANA: Lincoln, Ouachita, Richland. OKLAHOMA: McIntosh.

Remarks.—Because this species is so common and so widely distributed only the counties have been given in the above distribution records.

In northern Florida associated with the normal form is a much larger one which differs from it only in size. Normally the parents die as soon as the young leave the brood-pouch; but it is probable that in northern Florida there is a race which has a second brood. The larger specimens being those which had lived and continued to grow after their first young had left the brood-pouch and were having their second brood.

CRANGONYX GRACILIS PACKARDII S. I. Smith

1888. *Crangonyx packardii* S. I. Smith, Mem. Nat. Acad. Sci. 4:35.

1899. *Eucrangonyx packardii* (S. I. Smith). Stebbing, Trans. Linn. Soc. London II, 7:423.

Localities.—INDIANA: LAWRENCE Co.: stream in Shiloh Cave, 2 miles east of Fayetteville. CRAWFORD Co.: drip pool, below the "Throne," Wyandotte Cave, Wyandotte; stream in Sibert's Well Cave, Wyandotte. KENTUCKY: HART Co.: stream in Hidden River Cave, Horse Cave. ILLINOIS: SALINE Co.: stream in Cave Hill Cave, 2.9 miles west of Horseshoe. UNION Co.: stream in Wet Cave, near Roaring Spring, 6 miles south of Anna. KANSAS: FRANKLIN Co.: stock well, Wheeler farm, 5 miles south-south-east of Ottawa. MIAMI Co.: Yates well, 4 miles southwest of Osawatimie. BOURBON Co.: spring, 2.3 miles south of Bronson; seep, 2.2 miles east of Uniontown.

Remarks.—Since *C. packardii* differs from *C. gracilis* only in the degenerate eyes and absence of pigment it can hardly be considered to be specifically distinct.

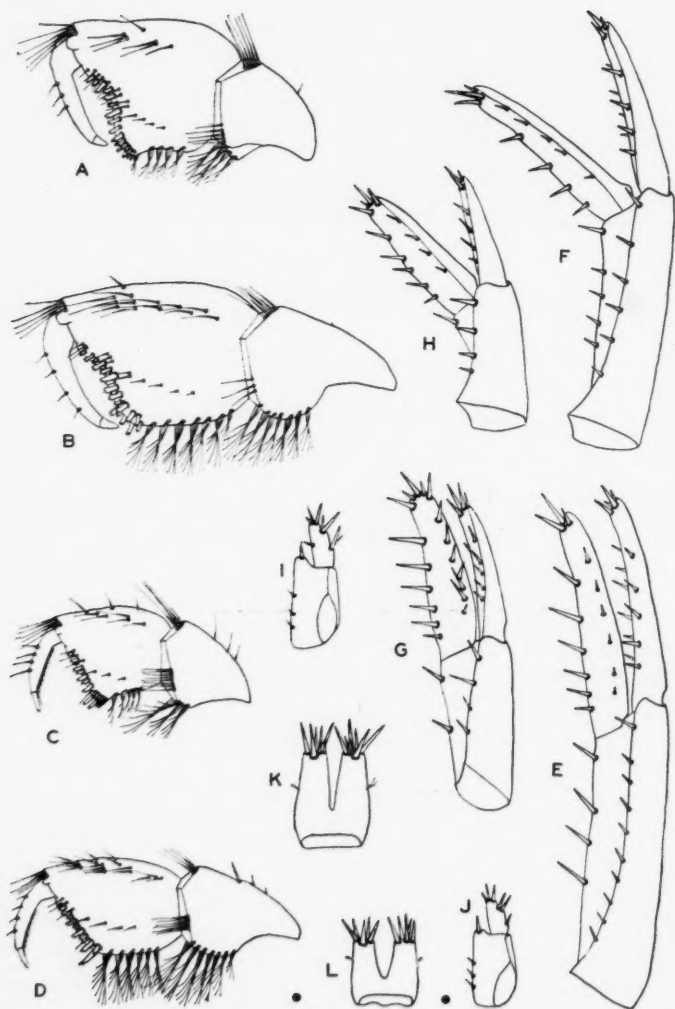


PLATE 2. *Synurella dentata*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, first uropod, female; G, second uropod, male; H, second uropod, female; I, third uropod, male; J, third uropod, female; K, telson, male; L, telson, female.

Genus *BACTRURUS* W. P. Hay1902. *Bactrurus* W. P. Hay, Proc. U. S. Nat. Mus. 25:430.*BACTRURUS MUCRONATUS* (Forbes)1876. *Crangonyx mucronatus* Forbes, Bull. Ill. State Lab. Nat. Hist. 1:6.1902. *Bactrurus mucronatus* (Forbes), W. P. Hay, Proc. U. S. Nat. Mus. 25:429.

Localities.—OHIO: LUCAS Co.: outlet of drain, 1.3 miles south of Reynolds Corners. WOOD Co.: outlet of drain, 1.3 miles southeast of Perryville. MARION Co.: outlet of drain, 2.4 miles southwest of Middlesboro. MONTGOMERY Co.: outlet of drain, 4.4 miles east of New Lebanon. PREBLE Co.: outlet of drain, 0.2 miles northwest of New Hope. MICHIGAN: MONROE Co.: outlet of drain, 0.5 mile north of Ottawa Lake; outlet of drain, 1.5 miles west-southwest of Dundee. INDIANA: NOBLE Co.: outlet of drains, 3.5, and 3.8 miles west of Knightstown. GRANT Co.: outlet of drain, 5 miles west of Jonesboro. ILLINOIS: HENDERSON Co.: outlet of drain, 3 miles east of Biggsville. WARREN Co.: outlet of drain, 5.2 miles east of Biggsville; outlet of drain, 2 miles southeast of Cameron. LASALLE Co.: outlet of drain, Gustave Engelhaupt farm, just north of Peru. KNOX Co.: outlet of drain, 2 miles north of Abingdon; outlet of drain, 3.1 miles north of St. Augustine; outlet of drain, 1.5 miles southeast of Williamsfield. PEORIA Co.: outlet of drain, 1.5 miles northeast of Laura. FULTON Co.: outlet of drain, 1.4 miles south of Avon. McDONOUGH Co.: outlet of drain, 3 miles south of Colmar; outlet of drain, 4.8 miles north of Macomb. SALINE Co.: stream in Cave Hill Cave, 2.9 miles west of Horseshoe. IOWA: WASHINGTON Co.: outlet of drains, 0.5, and 1 mile south of Haskins. HENRY Co.: outlet of drain, 1.7 miles south of Swedesboro; outlet of drain, 1.4 miles southeast of New London. DES MOINES Co.: outlet of drain, 0.2 mile northwest of Danville. MISSOURI: SHANNON Co.: drip-pool, small cave in Searcy Hollow, 5 miles north of Montier; stream, twilight, middle opening, Jam-Up Cave, 4 miles north-northwest of Montier. CARTER Co.: seep, bluffs along Current River, at mouth of Mill Creek, 4 miles northwest of Van Buren. DOUGLAS Co.: seep, 0.5 miles east of Twin Bridges.

BACTRURUS BRACHYCAUDUS Hubricht & Mackin1940. *Bactrurus brachycaudus* Hubricht & Mackin, Amer. Midl. Nat. 23:201, fig. 8.

Localities.—ILLINOIS: GREENE Co.: spring at base of bluff, 3 miles north of Eldred. PIKE Co.: small spring, 1 mile southeast of Pearl. UNION Co.: seep, near McCann School, 2.5 miles northeast of Aldridge. MISSOURI: RALLS Co.: stream in Fisher Cave, 5 miles south-southeast of New London. PIKE Co.: pool in cave, 0.2 mile north of Frankford. JEFFERSON Co.: seep, near large spring, 2 miles south of Plattin; stream in Anderson's Cave, 3.5 miles south of Antonia. STE. GENEVIEVE Co.: small spring, 4.6 miles southwest of Ste. Genevieve; stream in Kolm's Cave, 2.5 miles southwest of Ste. Genevieve; stream in Saltpetre Cave, 3 miles northwest of Minnith. STE. FRANCOIS Co.: stream in Shaver Cave, 1.5 miles north of Bonne Terre. FRANKLIN Co.: drip-pools, in Meramec Caverns, 2.5 miles southeast of Stanton. BOONE Co.: stream in Hunter Cave, 5 miles north-northwest of Ashland. MILLER Co.: small stream in Klugs Cave, 2.4 miles south of Marys Home. TEXAS Co.: small stream in Bat Cave, 7 miles northeast of Success.

Genus *SYNURELLA* Wrzesniewski1877. *Synurella* Wrzesniewski, Zeit. wiss. Zool. 28:403.*Synurella dentata*, sp. nov.

Plate 2

Description.—Males reach a body length of 19 mm., females 15 mm. Usually gray-blue in life, but sometimes lavender, brown, or greenish. Eyes irregular, oval to reniform.

First antenna slightly less than one-half as long as the body, with up to thirty articles in the flagellum in the male, and twenty-three in the female. Second antenna about one-half as long as the first antenna, with up to eight articles in the flagellum in the male and eleven in the female. Second antenna of mature males armed with three paddle-shaped sensory organs on the fourth segment of the peduncle, five on the fifth, and one each on the first five segments of the flagellum.

Second gnathopod larger than the first. Propodi of the gnathopoda of the male very thick, the palmar margins strongly concave, and armed on each side with fifteen to twenty notched spines. Propodi of the gnathopoda of the female moderately thin, the palmar margins slightly concave, and armed on each side with ten to twelve notched spines. Superior lateral setae usually in transverse rows of two to four but sometimes irregularly placed. Inferior lateral setae solitary or occasionally in pairs. Setae on the posterior margins in transverse rows. Inner margin of the dactylus unarmed in the male, and armed with six to ten teeth and an equal number of setae in the female.

Outer rami of the first and second uropoda nearly as long as the inner. Ramus of the third uropod about two-thirds as long as the peduncle and armed with six to eight spines.

Telson longer than broad, cleft about two-thirds the distance to the base. The lobes each armed with about six spires.

S. dentata differs from *S. bifurca* in the dentate dactylus of the female, in the concave palmar margins of both the gnathopoda of both sexes, and in the males being larger than the females.

Cotypes.—Collected from a small spring in a barnyard near an old mansion, 2.9 miles south-southwest of Jintown, Fayette Co., Kentucky. U. S. Nat. Mus. cat. no. 79328; and collection of the author.

Localities.—OHIO: PREBLE Co.: small stream, 2 miles west of West Alexandria; small stream, 3.3 miles southeast of New Hope. MONTGOMERY Co.: outlet of drain, 4.4 miles east of New London. CLINTON Co.: small spring, 0.7 miles southeast of Westboro. GREENE Co.: springs, John Bryan State Park, 2 miles west of Clifton. BROWN Co.: spring rill, 1.8 miles south of Georgetown; spring, 5 miles south of Georgetown. INDIANA: HENRY Co.: outlet of drain, 1.4 miles west of Straughn. KENTUCKY: MASON Co.: spring, 1.6 miles north of Washington. JEFFERSON Co.: Echo Farm spring, 3.8 miles west of Simpsonville. FRANKLIN Co.: small spring, just east of Bridgeport. WOODFORD Co.: small spring, 3 miles north of Versailles; Sunnyside Farm spring, 4.5 miles east of Versailles. BOURBON Co.: small spring, 2.8 miles southwest of Millersburg; spring, 5.7 miles southwest of Paris. FAYETTE Co.: spring, along Bryan Station Road, 0.3 miles northeast of Eastin Road, 3 miles northeast of Lexington; spring, 0.8 miles east of Fort Spring; small spring, 2.9 miles south-southwest of Jintown. JESSAMINE Co.: spring, 6.1 miles north of Nicholasville; spring, 2.7 miles north of Nicholasville. GARARD Co.: springs, 2 miles northwest of Lancaster. LINCOLN Co.: small spring, 1 mile south of Preachersville. TENNESSEE: TROUSDALE Co.: spring, 2.6 miles east of Castalian Springs.

Remarks.—In this species the males are frequently found carrying the females. A habit which the author has observed before in the Gammaridae only in the genus *Gammarus*.

SYNURELLA BIFURCA (O. P. Hay)

1882. *Crangonyx bifurcus* O. P. Hay, Amer. Nat. 16:145.
1902. *Niphargus bifurcus* (O. P. Hay). W. P. Hay, Proc. U. S. Nat. Mus. 25:429.
1907. *Eucrangonyx bifurcus* (O. P. Hay). Weckel, Proc. U. S. Nat. Mus. 32:32, fig. 4.
1936. *Stygobromus bifurcus* (O. P. Hay). Schellenberg, Mitt. Zool. Mus. Berlin. 22:37.
1940. *Synurella bifurca* (O. P. Hay). Hubricht & Mackin, Amer. Midl. Nat. 23:204.

Localities.—ALABAMA: TUSCALOOSA Co.: small spring, 3.2 miles west of Bucksville. BIBB Co.: slough of Haysop Creek, 1 mile southwest of Brent. MISSISSIPPI: SCOTT Co.: stream, 4.1 miles east of Forest. HINDS Co.: small stream, 2.4 miles east of Clinton. RANKIN Co.: slough 0.8 mile west of Pelahatchee. MISSOURI: BUTLER Co.: slough, 6.1 miles north of Neelyville. ARKANSAS: LAWRENCE Co.: roadside slough, 0.6 mile west of Hoxie. CRAIGHEAD Co.: small stream, 2.6 miles south of Apsipur. PHILLIPS Co.: slough, 0.5 mile southeast of Turner; temporary pool, 5.5 miles north of Barton. CALHOUN Co.: small stream, 3.7 miles south of Thornton. ARKANSAS Co.: slough, 2.7 miles east-northeast of Humphreys. JEFFERSON Co.: slough, 4.3 miles northeast of Altheimer. MONROE Co.: stream, 4.5 miles southwest of Clarendon; slough, 1.1 miles north of Holly Grove. DALLAS Co.: slough, 2 miles northeast of Fordyce. CROSS Co.: temporary pool, 2.3 miles north of Cherry Valley. LOUISIANA: CLAIBORNE Co.: seeps, 0.6 mile southeast of Junction City.

SYNURELLA CHAMBERLAINI (Ellis)

1941. *Stygobromus chamberlaini* Ellis, Charleston Mus. Leaf. no. 16, pp. 3-8, 2 figs.

Locality.—SOUTH CAROLINA: BERKELEY Co.: pond, Richmond Plantation, 2.4 miles south of Cordesville.

Remarks.—This species has more characters in common with *Synurella bifurca* than with any species of *Stygobromus* and despite its free pleon segments I believe it belongs in *Synurella*, rather than in *Stygobromus* as placed by the author.

Genus STYGOBROMUS Cope

1872. *Stygobromus* Cope, Amer. Nat. 6:422.

Stygobromus mackini, sp. nov.

Plate 3

Description.—Blind. Opaque white in life. Largest male 7 mm. in length, largest female 10 mm., exclusive of appendages. First antenna two-fifths as long as the body with four to twenty-one segments in the flagellum. Second antenna three-fifths as long as the first antenna with two to six segments in the flagellum.

Palmar margins of the propodi of the gnathopoda very oblique, continuous with the posterior margin, straight or slightly convex, except the first gnathopod of the female in which it is slightly concave, and armed on each side with twelve to sixteen notched spines. Posterior margin short and armed with one to five transverse rows of setae. Propodi of the first and second gnathopoda about equal in size, but slightly different in shape. Carpus of the second gnathopod longer than that of the first in both sexes.

Outer rami of the first and second uropoda about as long as the inner. Peduncles of the first and second uropoda armed distally on their inner angles

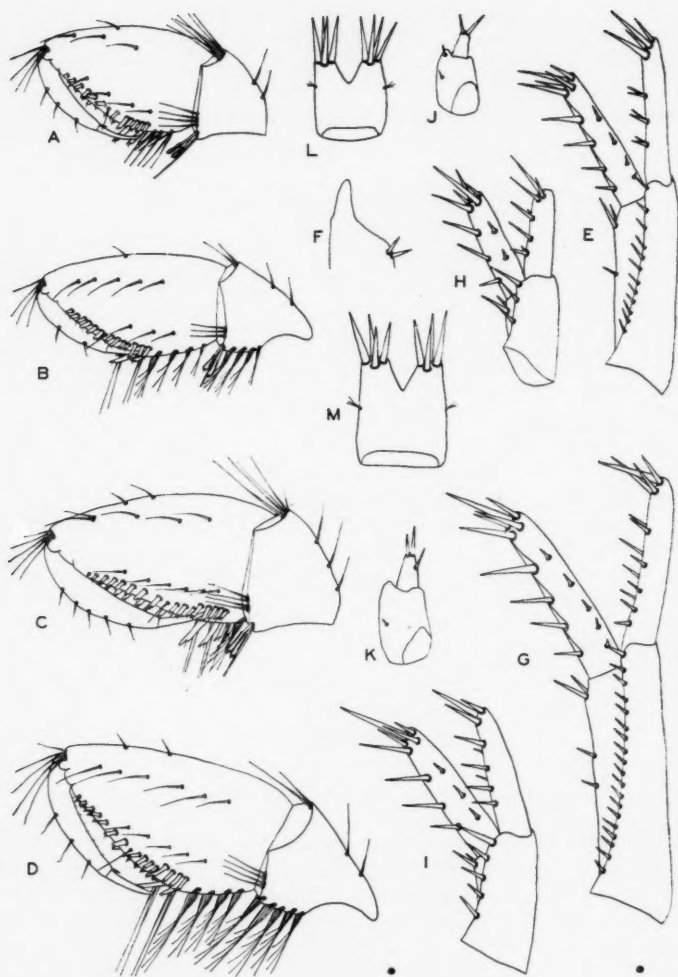


PLATE 3. *Stygobromus mackini*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, distal process of peduncle of first uropod, male; G, first uropod, female; H, second uropod, male; I, second uropod, female; J, third uropod, male; K, third uropod, female; L, telson, male; M, telson, female.

with two spines in both sexes. Peduncle of the first uropod of the male armed distally with a short, narrow, thin process, about one-fourth as long as the rami. Ramus of the third uropod about one-half as long as the peduncle and armed distally with two or three spines, and sometimes with a lateral spine. Peduncle with a single long spine on the lower distal margin (not shown in figure).

Telson a little longer than broad, cleft about one-third the distance to the base, each lobe armed with about four spines.

S. mackini is not closely related to any other species in the genus. It is distinguished by its large size, by the characters of the gnathopoda, and by the deeply cleft telson.

Named in honor of Dr. J. G. Mackin, Professor of Biology, East Central State Teachers College, Ada, Oklahoma.

Cotypes.—Taken from a pond in Sikes Cave, 4.5 miles north of Lebanon, Russell Co., Virginia. U. S. Nat. Mus. cat. no. 79324; and collection of the author.

Localities.—VIRGINIA: TAZEVELL Co.: pool in Chimney Cave, 2.3 miles southwest of Pounding Mill. RUSSELL Co.: pond in Sikes Cave, 4.5 miles north of Lebanon. TENNESSEE: GRAINGER Co.: stream in Indian Cave, 8 miles east of Blaine.

STYGOBROMUS VITREUS Cope

1872. *Stygobromus vitreus* Cope, Amer. Nat. 6:422.

1888. *Crangonyx vitreus* (Cope). S. I. Smith, Mem. Nat. Acad. Sci. 4:34, P. 5, figs. 1-4.

1909. [non] *Crangonyx vitreus* (Cope). Holmes, Trans. Wisc. Acad. Sci. 16:78, Pl. 7.

Localities.—KENTUCKY: EDMONSON Co.: Richardson's Spring, Mammoth Cave; drip pools, White's Cave, near Mammoth Cave; stream in Cedar Sink Cave, 5 miles southwest of Mammoth Cave P. O. ALABAMA: MADISON Co.: drip pool, Aladdin Cave, Sharps Cove, 8 miles northeast of Maysville.

STYGOBROMUS SPINOSUS (Hubricht & Mackin)

1940. *Crangonyx spinosus* Hubricht & Mackin, Amer. Midl. Nat. 23:203-205, fig. 10.

Locality.—VIRGINIA: PAGE Co.: drip pools, Luray Caverns, Luray.

Remarks.—More than a hundred specimens were collected at the above locality, none of which were males. Several similar lots of females have been collected in other species, which strongly suggests the presence of parthenogenesis in this genus.

Stygobromus exilis, sp. nov.

Plate 4

1909. *Crangonyx vitreus* (Cope). Holmes, Trans. Wisc. Acad. Sci. 16:78, Pl. 7.

Description.—Blind. Opaque white or cream colored in life. Both sexes about the same size, 4 mm. in length, exclusive of appendages. Flagellum of the first antenna with up to twelve segments, that of the second antenna with up to three segments.

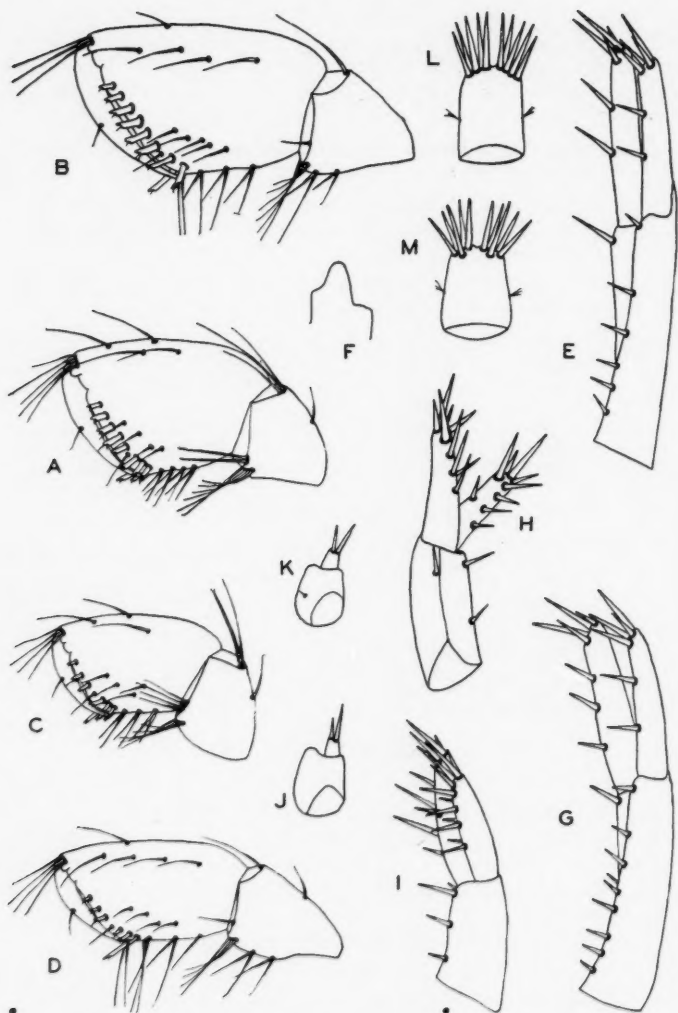


PLATE 4. *Stygobromus exilis*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, distal process of peduncle of first uropod, male; G, first uropod, female; H, second uropod, male; I, second uropod, female; J, third uropod, male; K, third uropod, female; L, telson, male; M, telson, female.

Palmar margins of the propodi of the gnathopoda straight or slightly concave, separated from the posterior margin by an obtuse angle, and armed on each side with about eight notched spines in the male, and about six in the female. Posterior margins about as long as the palmar margins, and armed with six to eight setae, which are usually in pairs. Propodus of the first gnathopod only slightly smaller than that of the second in both sexes. Carpus of the second gnathopod distinctly longer than that of the first in the female.

Peduncle of the first uropod of the male produced distally into a rounded, thin lobe, about one-fifth the length of the rami. Outer ramus of the first uropod slightly shorter than the inner ramus. Outer ramus armed with two spines on the outer edge, inner edge unarmed. Inner ramus armed with two or three spines on the inner edge, outer edge unarmed. Outer ramus of the second uropod about three-fourths as long as the inner ramus, usually a little more spiny than those of the first uropod. Ramus of the third uropod about one-third as long as the peduncle and armed distally with usually two spines.

Telson a little longer than broad, the posterior margin rounded with a slight central notch, and armed with about ten spines.

Stygebromus exilis can be readily distinguished from *S. vitreus*, which occurs in the same region, by its smaller propodi of the gnathopoda, and by the long carpus on the second gnathopod of the female. It is most closely related to *Stygebromus onondagaensis*.

Cotypes.—From a drip-pool in Mammoth Onyx Cave, 3 miles north of Horse Cave, Hart Co., Kentucky. U. S. Nat. Mus. cat. no. 79325; and collection of the author.

Localities.—KENTUCKY: HART CO.: drip-pool, Mammoth Onyx Cave, 3 miles north of Horse Cave. EDMONSON CO.: stream in Cedar Sink Cave, 5 miles southwest of Mammoth Cave P. O. TENNESSEE: HAMILTON CO.: stream in Ruby Falls Cave, near Chattanooga. BLOUNT CO.: drip-pools, Gregory's Cave, Cades Cove. ALABAMA: BIBB CO.: S. C. Roden's well, Woodstock.

Remarks.—The series of over a hundred specimens from Gregory's Cave is all females.

STYGOBROMUS ONONDAGAENSIS (Hubricht & Mackin)

1940. *Crangonyx onondagaensis* Hubricht & Mackin, Amer. Midl. Nat. 23:202-203, fig. 9.

Localities.—MISSOURI: WASHINGTON CO.: stream in Hamilton Cave, 5.5 miles southeast of Sullivan. FRANKLIN CO.: drip-pools, Mushroom Cave, 2.5 miles east of Sullivan; seep, 0.5 mile northwest of Mushroom Cave. ST. FRANCOIS CO.: small spring, 2 miles north-northeast of Bismarck. WAYNE CO.: drip-pool, Holmes Cave, 4.5 miles east of Patterson. CRAWFORD CO.: pools in Onyx Cave, in bluff above Brazil Creek, 3 miles north of Campbell Bridge, 8 miles southeast of Bourbon. SHANNON CO.: stream in Cave Hollow Cave, near Ebb and Flow Spring, 6 miles north of Montier; drip-pool, Branson Cave, 1 mile northwest of Alley; drip-pool, Medlock Cave, 2 miles northwest of Akers. CARTER CO.: stream in Cave Spring Onyx Cave, 2 miles west of Van Buren. PHELPS CO.: stream in Saltpeter Cave, 7 miles north of Newburg; stream in Marcellus Cave, 5 miles south of St. James; stream in Easter Cave, 8 miles northwest of Rolla. PULASKI CO.: drip-pools, in Maxey Cave, 1.5 miles north of Hanna; drip-pool, in

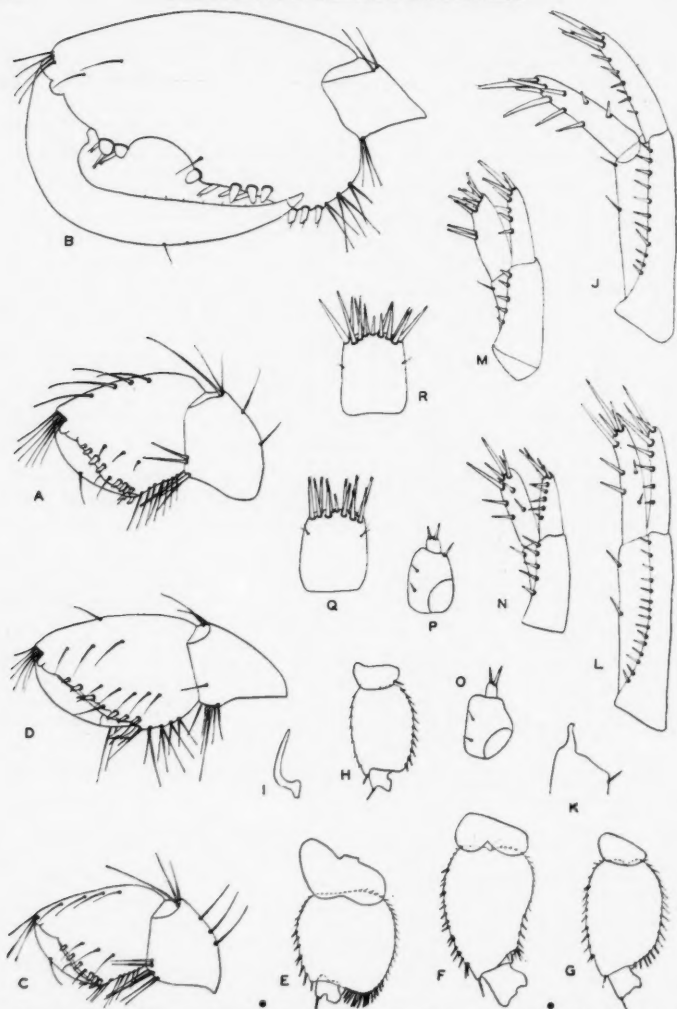


PLATE 5. *Stygobromus heteropodus*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first three segments of third peraeopod, male; F, first three segments of fourth peraeopod, male; G, first three segments of fifth peraeopod, male; H, first three segments of fifth peraeopod, female; I, sternal gill; J, first uropod, male; K, distal process of peduncle of first uropod, male; L, first uropod, female; M, second uropod, male; N, second uropod, female; O, third uropod, male; P, third uropod, female; Q, telson, male; R, telson, female.

Spring Cave, 5 miles south of Crocker. CAMDEN Co.: drip-pool, River Cave, Hahatonka. MILLER Co.: small stream, in a small cave, 0.3 mile southeast of Miller County Home, 3 miles southeast of Tusculumbia. KANSAS: BUTLER Co.: Purity Springs, 3.3 miles east of Augusta. OKLAHOMA: MAYES Co.: seep, Girl Scout Camp, 3.2 miles south of Locust Grove.

STYGOBROMUS PUTEALIS (Holmes)

1908. *Crangonyx putealis* Holmes, Trans. Wisc. Acad. 16:77, pl. 6-7.

1936. *Stygobromus putealis* (Holmes). Schellenberg, Mitt. Zool. Mus. Berlin. 22:37.

Localities.—WISCONSIN: FOND DU LAC Co.: wells, Rosendale; wells, 0.5 mile east of Ripon. DODGE Co.: wells, 1 to 2 miles south of Waupun.

Remarks.—This species is unique in being without sternal gills. The four sternal gills are replaced by two blister-like organs on the sternum.

Stygobromus heteropodus, sp. nov.

Plate 5

Description.—Blind. Opaque white in life. Largest male 7 mm. in body length, largest female 6 mm. First antenna a little more than two-thirds as long as the body. Second antenna about one-half as long as the first.

Palmar margins of the propodi of the first gnathopoda somewhat sigmoid, concave anteriorly and convex posteriorly, separated from the posterior margin by an obtuse angle, and armed on each side with six to eight notched and ciliated spines. Propodus of the second gnathopod of the male much enlarged, the palmar margin very oblique with a deep excavation, armed on the inner margin with six or seven bluntly rounded spines, and on the outer margin with eight to ten notched and ciliated spines. Propodus of the second gnathopod of the female somewhat larger than the first but not as large as in the male, the palmar margin oblique, irregularly scalloped, and armed on each side with six to eight notched and ciliated spines. Setae on the posterior margins of the propodi of the second gnathopoda in three or four transverse rows, usually solitary on the first gnathopoda.

Second segment of the third pereopod of the male about as broad as long, the posterior distal margin convex and armed with numerous long, ciliated spines. That of the fourth pereopod about one and one-half times as long as broad, with the posterior distal margin concave. That of the fifth pereopod similar to the fourth but with the posterior distal margin convex. Second segments of the third, fourth, and fifth pereopoda in the female similar to the fifth of the male.

Peduncle of the first uropod of the male produced distally into a long, thin lobe about one-fourth the length of the rami. Peduncles of the first and second uropoda armed with one spine distally on the inner angle. Outer rami of the first and second uropoda slightly shorter than the inner rami. Ramus of the third uropod about one-fourth as long as the peduncle and armed distally with two or three spines.

Telson a little longer than broad, without an emargination in the distal margin, and armed with ten to fifteen spines.

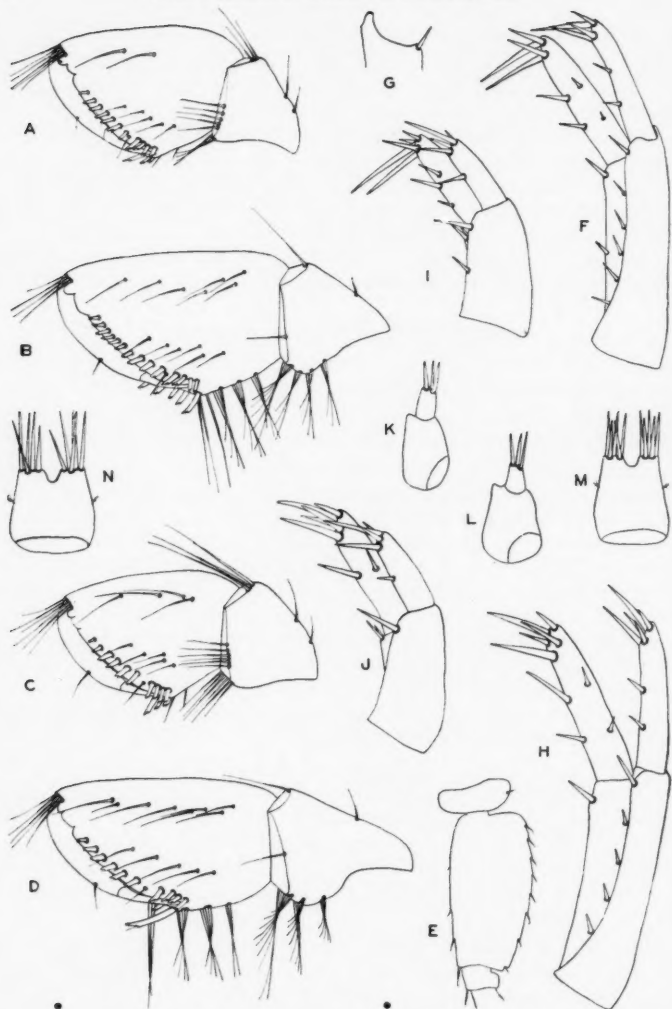


PLATE 6. *Stygobromus iowae*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first three segments of fifth pereopod, male; F, first uropod, male; G, distal process of peduncle of first uropod, male; H, first uropod, female; I, second uropod, male; J, second uropod, female; K, third uropod, male; L, third uropod, female; M, telson, male; N, telson, female.

Unlike other species in the genus the sternal gills are sickle-shaped and show quite plainly the mode of development of the bifurcate gills of *Synpletonia*. Some other species of the genus have curved or twisted gills but they do not have the distinct 'handle' and 'blade' of this species. The deep excavation in the palmar margin of the second gnathopod of the male, and the peraeopoda will distinguish this species from any other described species in the genus.

Cotypes.—Collected in a small spring under a ledge in the main valley, Pickle Springs, head of Pickle Creek, Genevieve Co., Missouri. U. S. Nat. Mus. cat. no. 79412; and collection of the author.

***Stygobromus iowae*, sp. nov.**

Plate 6

Description.—Blind. Light straw colored in life. Sexes similar. Largest male 6 mm. in body length, largest female 7 mm. First antenna one-third as long as the body. Second antenna one-half as long as the first.

Palmar margins of the propodi of the first gnathopoda oblique, slightly convex and armed on each side with ten to fifteen notched and ciliated spines. Lateral setae solitary, the posterior margins without setae. Propodi of the second gnathopoda similar but longer, and with three or four transverse rows of setae on the posterior margin. Carpus of the second gnathopod of the female distinctly longer than that of the male.

The second segments of the third, fourth, and fifth peraeopoda similar in both sexes, about twice as long as broad.

Peduncle of the first uropod of the male armed distally with a short rounded lobe, about one-tenth as long as the rami. Rami of the first uropoda subequal. Outer ramus of the second uropod about two-thirds as long as the inner. Outer rami of the first and second uropoda armed with five to eight spines, the inner rami with six to ten. Distal inner angle of the peduncle of the first uropod with a single spine, that of the second with two spines. Ramus of the third uropod almost one-half as long as the peduncle and armed distally with three spines.

Telson a little longer than wide, distinctly cleft distally, each lobe armed with about five spines.

This species seems most closely related to *S. onondagaensis* and *S. exilis*. It can readily be distinguished from these by the gnathopoda and by the distinctly cleft telson.

Cotypes.—Collected in a spring, 0.7 miles north of Fayette, Fayette Co., Iowa. U. S. Nat. Mus. cat. no. 79411; and collection of the author.

***Stygobromus smithi*, sp. nov.**

Plate 7

Description.—Blind. Pale straw-colored in life. Sexes similar. Largest male 9 mm. in body length, largest female 10 mm. First antenna one-half as long as the body, second antenna one-half as long as the first.

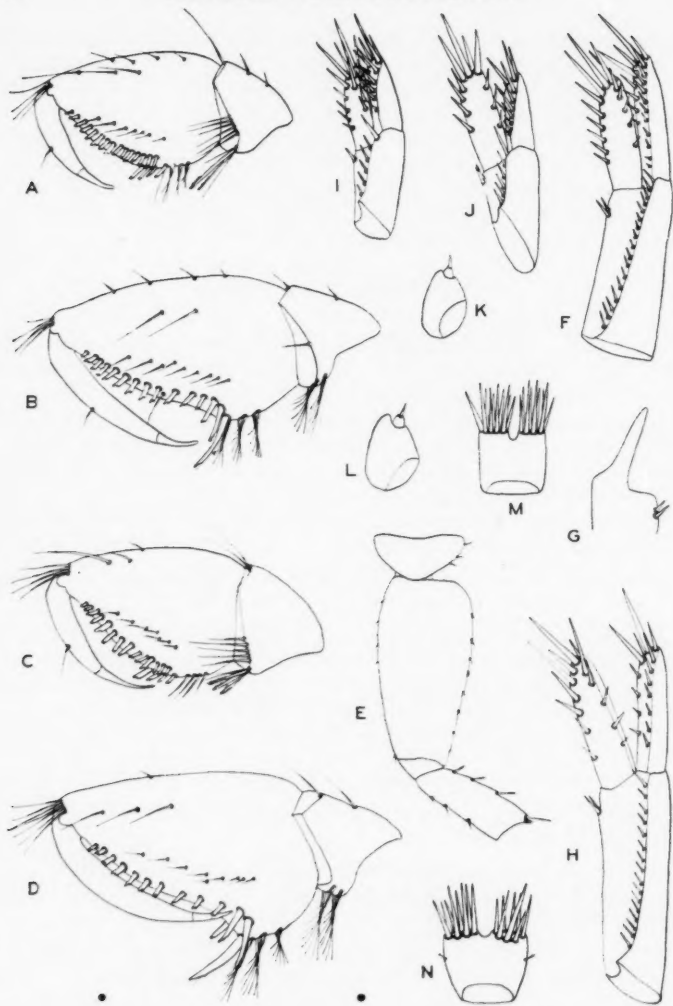


Plate 7. *Stygobromus smithi*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first three segments of fifth pereopod, male; F, first uropod, male; G, distal process of peduncle of first uropod, male; H, first uropod, female; I, second uropod, male; J, second uropod, female; K, third uropod, male; L, third uropod, female; M, telson, male; N, telson female.

Palmar margin of the propodus of the first gnathopod convex, continuous with the posterior margin and armed on each side with twelve to fifteen notched and ciliated spines. The posterior margin armed with solitary setae in the female and three transverse rows in the male. Palmar margins of the second gnathopoda slightly sigmoid, separated from the posterior margin by a distinct angle, and armed on each side with twelve to fifteen notched and ciliated spines. The posterior margin armed with three transverse rows of setae. Carpus of the female not longer than that of the male.

Second segments of the third, fourth, and fifth pereopoda similar, about twice as long as wide.

Peduncle of the first uropod of the male armed distally with a long slender process about two-thirds as long as the rami. Outer rami of the first and second uropoda as long as or a little longer than the inner rami. Outer ramus of the first uropod armed with fifteen to twenty unusually long spines, the inner ramus with ten to fifteen. Rami of the second uropod armed with ten to fifteen spines each. Peduncles of the first and second uropoda armed with usually two spines distally on the inner angle. Ramus of the third uropod vestigial and armed with a single spine.

Telson about as long as broad, with a distinct distal notch, each lobe armed with eight to ten spines.

This species is apparently related to *S. vitreus* from which it may be distinguished by its larger size, vestigial ramus of the third uropod, more spiny telson, and differences in the gnathopoda.

Named in honor of the late Professor Sidney I. Smith, of Yale.

Cotypes.—Collected in S. C. Roden's well, Woodstock, Bibb Co., Alabama. U. S. Nat. Mus. cat. no. 79410; and collection of the author.

Localities.—ALABAMA: TUSCALOOSA Co.: seep, 2.6 miles south of Samantha School. BIBB Co.: S. C. Roden's well, Woodstock.

Remarks.—In drip-pools in Gregory's Cave, Cades Cove, Blount Co., Tennessee, there occurs an amphipod which is identical with this species except that the third uropod is without a ramus and the males do not have a distal process on the peduncle of the first uropod.

Genus STYGONECTES W. P. Hay

1902. *Stygonectes* W. P. Hay, Proc. U. S. Nat. Mus. 25:429.

STYGONECTES FLAGELLATUS (Benedict)

1896. *Crangonyx flagellatus* Benedict, Proc. U. S. Nat. Mus. 18:616.

1902. *Stygonectes flagellatus* (Benedict). W. P. Hay, Proc. U. S. Nat. Mus. 25:429.

Localities.—TEXAS: HAYS Co.: artesian well at Fish Hatchery, San Marcos. KENDALL Co.: pool in Cascade Cave, 5 miles east of Boerne; stream in Cave Without a Name, 11 miles northeast of Boerne.

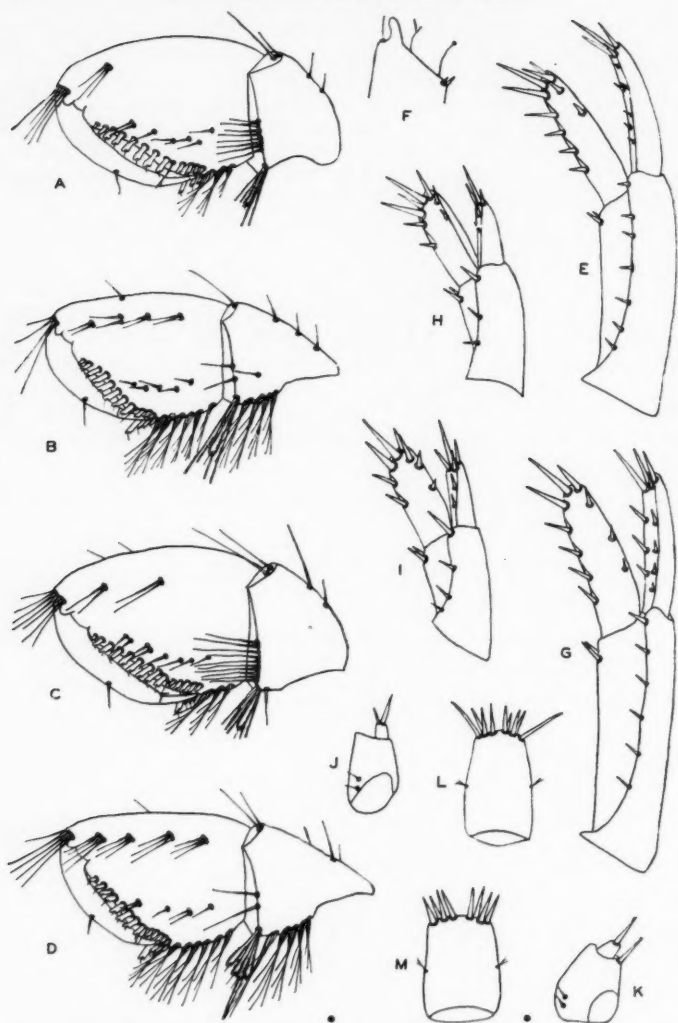


PLATE 8. *Stygonectes balconis*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, distal process of peduncle of first uropod, male; G, first uropod, female; H, second uropod, male; I, second uropod, female; J, third uropod, male; K, third uropod, female; L, telson, male; M, telson, female.

Stygonectes balconis, sp. nov.

Plate 8

Description.—Blind. Straw-colored in life. Largest male 12 mm. in body length, largest female 12.5 mm. First antenna one-half as long as the body, second antenna one-half as long as the first.

Palmar margins of the propodi of the gnathopoda concave, gradually rounding into the posterior margins, and armed on each side with from ten to fifteen notched and ciliated spines. Superior lateral setae in short transverse rows of two to five. Inferior lateral setae solitary or in pairs. Setae on the posterior margins in transverse rows. First gnathopoda stouter but not much larger than the second.

Distal end of the peduncle of the first uropod of the male produced into a thin, rounded lobe. Outer ramus of the first uropod slightly shorter than the inner ramus. Inner margins of the inner rami of the first and second uropoda armed with usually two spines. Outer ramus of the second uropod about two-thirds as long as the inner ramus. Ramus of the third uropod about one-fourth as long as the peduncle and armed with one or two spines.

Telson about one and one-half as long as broad, the posterior margin slightly convex and armed with eight to ten spines.

The resemblance of this species to *Synpleonia americana* is remarkable. Were it not for the differences in the sternal gills they could not be distinguished except by the difference in size.

Cotypes.—Collected by Dr. J. G. Mackin, from drip-pools in Boyett's Cave, on highway 80, 14 miles northwest of San Marcos, Hays Co., Texas. U. S. Nat. Mus. cat. no. 79323; and collection of the author.

Localities.—TEXAS: HAYS CO.: drip-pools in Boyett's Cave, on highway 80, 14 miles northwest of San Marcos. KENDALL CO.: pool in Cave Without a Name, 11 miles northeast of Boerne.

Genus *SYNPLEONIA* Creaser

1934. *Synpleonia* E. P. Creaser, Occas. Papers Mus. Zool. Univ. Mich. no. 282, p. 1.

Synpleonia emarginata, sp. nov.

Plate 9

Description.—Blind. Opaque white to straw-colored in life. Largest female 13 mm., largest male 9 mm. in body length. Flagellum of the first antenna with up to twenty-two segments, that of the second antenna with up to eight.

Male and female gnathopoda similar. Palmar margin of the propodus of the first gnathopod convex, very oblique, continuous with the posterior margin, and armed with twelve to fifteen notched spines on each side. Posterior margin very short, unarmed. Palmar margin of the propodus of the second gnathopod convex, not as oblique as the first, separated from the posterior margin by an

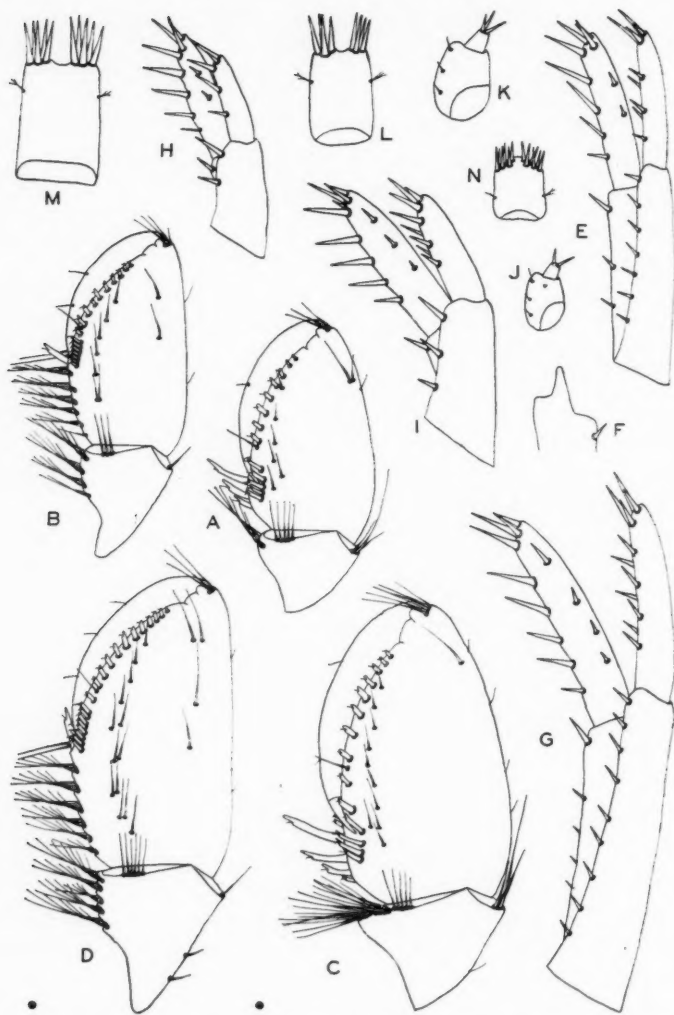


PLATE 9. *Synpleonia emarginata*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, distal process of peduncle of first uropod, male; G, first uropod, female; H, second uropod, male; I, second uropod, female; J, third uropod, male; K, third uropod, female; L, telson, male; M, telson, female; N, telson, immature.

obtuse angle, and armed with from fifteen to twenty notched spines. Posterior margin about two-fifths as long as the palmar margin and armed with about six transverse rows of setae. Lateral setae solitary or in pairs on both gnathopoda. Carpus of the second gnathopod longer than that of the first.

Second segment of the fifth pereopod of the male not produced into a rounded lobe anteriorly, but with a posterior lobe. Not distinguishable from that of the female.

Peduncle of the first uropod of the male produced distally into a slender, thin lobe, about one-fifth the length of the rami. Outer ramus slightly shorter than the inner ramus in both sexes. Outer ramus of the second uropod about three-fourths as long as the inner ramus. Peduncles of the first and second uropoda armed distally on the inner angles with a single spine; the rami armed on each side with two to five spines. Ramus of the third uropod about one-third as long as the peduncle and armed distally with two or three spines.

Telson of mature specimens about one and one-third as long as broad, with a broad shallow emargination in the posterior margin, each lobe armed with four or five spines. Telson of immature specimens slightly longer than broad, the posterior margin convex, without an emargination.

S. emarginata may be readily distinguished from other species of the genus by the short, unarmed posterior margin of the propodus of the first gnathopod, and by the emarginate telson. It is probably most closely related to *S. hayi*.

Cotypes.—From a stream in Organ Cave, near Organ Cave P. O., Greenbrier Co., West Virginia. U. S. Nat. Mus. cat. no. 79327; and collection of the author.

Localities.—WEST VIRGINIA: GREENBRIER CO.: stream in Organ Cave, near Organ Cave P. O.; stream in Hayes Cave, just north of Lewisburg.

Remarks.—The last three pleon segments are definitely fused in adults but the sutures are visible. They apparently are not fused in the young.

The lot from Hayes Cave is composed of a large number of morphologically immature but sexually mature females. A number of which had eggs in their brood-pouches, although no males were found.

SYNPLEONIA HAYI Hubricht & Mackin

1940. *Synpleonina hayi* Hubricht & Mackin, Amer. Midl. Nat. 23:205, fig. 11.

Localities.—PENNSYLVANIA: CENTRE CO.: Penn's Cave. FAYETTE CO.: Barton Cave; Dulany Cave.

The above material was collected by Mr. Kenneth Dearolf.

SYNPLEONIA PIZZINII Shoemaker

1938. *Synpleonina pizzinii* Shoemaker, Proc. Biol. Soc. Wash. 51:137.

Localities.—VIRGINIA: WARREN CO.: stream in Skyline Caverns, 2 miles south of Front Royal. ROCKINGHAM CO.: drip-pool, Massanutten Caverns, near Keezletown.

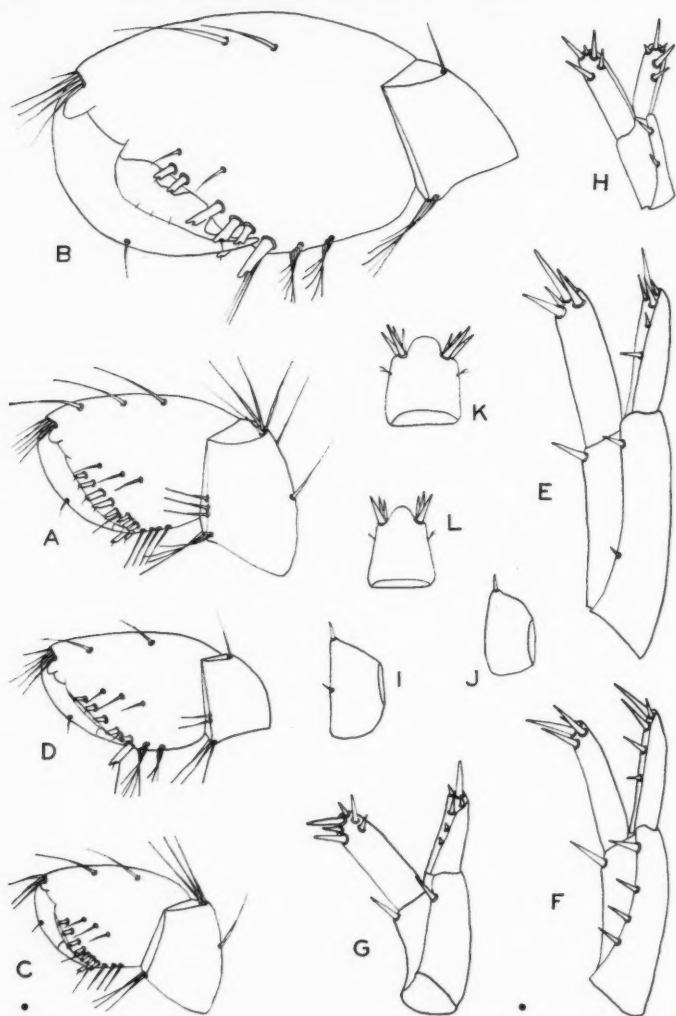


PLATE 10. *Apocrangonyx subtilis*, sp. nov. A, first gnathopod, male; B, second gnathopod, male; C, first gnathopod, female; D, second gnathopod, female; E, first uropod, male; F, first uropod, female; G, second uropod, male; H, second uropod, female; I, third uropod, male; J, third uropod, female; K, telson, male; L, telson, female.

SYMPLEONIA CLANTONI Creaser

1934. *Synpleonion clantoni* Creaser, Occas. Papers Mus. Zool. Univ. Mich. no. 282, p. 2, pl. 1.
1940. [non] *Synpleonion clantoni* Creaser. Hubricht & Mackin, Amer. Midl. Nat. 23:206.

Localities.—MISSOURI: STONE Co.: Blondys Throan, in cave stream part, Marvel Cave (Byron C. Marshall, coll.). ARKANSAS: LOGAN Co.: seep, 0.2 mile east of The Lodge, Magazine Mtn. KANSAS: FRANKLIN Co.: Dunkak's well, 1.5 miles northwest of Lane. BOURBON Co.: seep, 2.3 miles south of Bronson. BUTLER Co.: pools, cave, 6 miles south of El Dorado; Purity Springs, 3.3 miles east of Augusta. OKLAHOMA: MAYES Co.: seep, Girl Scout Camp, 3.2 miles south of Locust Grove.

SYMPLEONIA AMERICANA (Mackin)

1935. *Boruta americana* Mackin, Trans. Amer. Micro. Soc. 54:46, pl. 10.
1936. *Synpleonion americana* (Mackin). Schellenberg, Mitt. Zool. Mus. Berlin. 22:40.
1940. *Synpleonion clantoni* Creaser. Hubricht & Mackin, Amer. Midl. Nat. 23:206.

Localities.—MISSOURI: PULASKI Co.: stream in Bat Cave, 5 miles south of Crocker. PHELPS Co.: temporary spring, 1 mile west of Hooker. LACLEDE Co.: seep, near Bennett Spring. WRIGHT Co.: pools, Smittle Cave, 5 miles north of Grove Spring. BARRY Co.: small stream, Crystal Caverns, near Cassville. NEWTON Co.: seep, near Big Spring, Neosho. ARKANSAS: VAN BUREN Co.: seep, 5.5 miles north of Clinton. BENTON Co.: seep, near Big Spring, Bella Vista. WASHINGTON Co.: seeps, 1.5 miles north of Winslow. LOGAN Co.: seep, 0.6 mile east of The Lodge, Magazine Mtn. OKLAHOMA: MAYES Co.: seeps, 4.6 miles west of Locust Grove.

Remarks.—In the author's first paper this species was placed in the synonymy of *S. clantoni*. However, it is quite distinct and all of the records for *S. clantoni* in that paper belong under *S. americana*.

SYMPLEONIA ALABAMENSIS (Stout)

1911. *Crangonyx alabamensis* Stout, Pomona Coll. Jour. Entom. 3:569, figs. 187-188.
1936. ? *Synpleonion alabamensis* (Stout). Schellenberg, Mitt. Zool. Mus. Berlin. 22:40.

Locality.—ALABAMA: LEE Co.: well, L. B. Yarbrough Dairy (NW $\frac{1}{4}$; S29; T19N; R26E), 1 mile east of the Post Office, Auburn.

Remarks.—The author received two mature males of this species from Prof. J. M. Robinson, Alabama Polytechnic Institute, Auburn, and later visited the well with him and collected a large series. The species is remarkably close to *S. americana*, the gnathopoda, uropoda, and telson being almost indistinguishable. The body is much more slender, however, and the first antenna of the male are much longer, being almost as long as the body.

Genus APOCRANGONYX Stebbing

1899. *Apocrangonyx* Stebbing, Trans. Linn. Soc. London II, 7:422.

Apocrangonyx subtilis, sp. nov.

Plate 10

Description.—Blind. Flesh-colored in life. Males reach a body length of 5 mm., females 4 mm. First antenna about two-fifths as long as the body, with

up to twelve segments in the flagellum. Second antenna about one-half as long as the first antenna, with up to five segments in the flagellum.

Palmar margin of the propodus of the first gnathopod of the male straight, armed on each side with about eight notched spines, and separated from the posterior margin by an obtuse angle. Propodus of the second gnathopod of the male much larger than the first, the palmar margin strongly concave, gradually curving into the posterior margin, with a prominent, thin, bidentate process in the middle and a smaller one opposite the claw, and armed on each side with about six notched spines. Propodus of the second gnathopod of the female slightly larger than the first, the palmar margin more oblique and gradually curving into the posterior margin. Setae on the posterior margins solitary on the first gnathopod and in two transverse rows on the second. Lateral setae few and solitary. Carpus of the first gnathopod slightly larger than that of the second in both sexes.

Sternal gills on the sixth and seventh thoracic segments, bifurcate as in *Synpleonia*.

Urosome completely fused. The sutures not visible.

Outer rami of the first and second uropoda slightly shorter than the inner rami. Rami with lateral spines except on the outer margin of the outer ramus. Peduncle of the first uropod without a distal process. Third uropod reduced to a thin plate attached by the lateral margin and carried folded inward to form a door over the anus.

Telson about as broad as long, armed distally with a thin, rounded process, and four or five spines on each posterior-lateral angle.

A. lucifugus (O. P. Hay) differs from this species in the following characters: the propodi of the second gnathopoda are twice as long as broad; the inner ramus of the second uropod is nearly twice as long as the outer; the telson is without the distal process.

Cotypes.—From a small seep on the east wall of the first sandstone sink west of Bat Cave Sink, 5 miles southwest of Pomona, Jackson Co., Illinois. U. S. Nat. Mus. cat. no. 79346; and collection of the author.

Localities.—ILLINOIS: JERSEY CO.: small seep on hillside, 8.5 miles west of Grafton. MONROE CO.: drip-pool, "The Pit," cave on bluff, just north of Fults. JACKSON CO.: small seep on east wall of first sandstone sink west of Bat Cave Sink, 5 miles southwest of Pomona. UNION CO.: small seep on sandstone bluff, 1 mile south of Alto Pass.

Biology of a Mull-forming Millipede, *Apheloria coriacea* (Koch)

Theodore H. Eaton, Jr.

During a study of the fauna of forest soils with Prof. R. F. Chandler, Jr., Department of Agronomy, Cornell University, the author made the observations reported here on the development and activities of *Apheloria coriacea*. No account of its life-history has been published hitherto, but Romell (1935) noted it, with *A. trimaculata*, as a mull-forming species at North Hudson, New York.

Mull is a type of humus layer in which organic matter is mixed thoroughly with the upper mineral soil. In the northeastern states mull is the more common humus layer type in deciduous forests, while mor or duff humus layers (a surface layer of unincorporated organic matter) are generally present in coniferous forests. This distinction is not absolute, since other factors than vegetation also affect the humus layer.

Apheloria coriacea (Koch) is a common and conspicuous millipede of the northeastern and north-central states. The adults are 30-45 mm. long and 6-9 mm. wide, with the segments arched, not ring-shaped, so that the animal appears convex but not cylindrical. The dorsal surface is dark brown with contrasting yellow to orange bands on the posterior margins of the segments. The projecting lateral flanges are orange or pink, while the legs and entire under side are pale yellow. The closely related *A. trimaculata* of the same region differs in having three yellow spots instead of a band for each segment, and in details of the male clasping organs (gonopods, a modified pair of appendages on the seventh segment).

Historical Review and Distribution

The Fontariid millipedes, a North American family, appear first in the literature with Drury's (1770) illustration of *Julus virginianensis*. Gray figured the same species in Griffith's (1832) translation of Cuvier's *Regne Animal*, with the generic name *Fontaria*. *F. coriacea* was described by Koch (1847), likewise from Virginia. Wood (1864), unaware of Koch's work, described the same species as *Polydesmus corrugatus*, from Michigan and New York. Bollman (1888) noted that Wood's species was synonymous with Koch's, and added records from Indiana. In 1921 Chamberlin erected the genus *Apheloria* "for a group of species, heretofore included in *Fontaria*, in which the telopodite of the gonopod of male is a simple, coiled blade with a small spur at base. Genotype—*Fontaria montana* (Bollman)." Although *coriacea* and *trimaculata* are not mentioned here, both possess this character.

A. coriacea appears in the New York State list of insects and related groups (Bailey, 1928) as *F. corrugatus* (Wood), with ten locality records. In

the same year Williams and Hefner described it from Ohio, with the name *Fontaria coriacea* Koch. Romell (1935) discussed its mull-forming activities in northeastern New York. It is listed by Brimley (1938) from the Duke Forest, North Carolina, and by Loomis (1939) from Cave City, Kentucky.

Many other species have been described, and several new genera proposed, allied to or originally placed in *Fontaria*. Although they occur from Mexico to Canada, and from the Atlantic to the Pacific, the greater number are southeastern, centering in the humid forests of the southern Appalachians. The distribution of Fontariidae thus shows an interesting parallel to that of the Plethodontid salamanders; ecologically the two have much in common.

Observations by Romell on Mull Formation

Near North Hudson, New York, on a "steep south slope carrying a stand of middle-aged white pine with hardwood undergrowth and a ground vegetation of Heimbürger's *Dicentra* type," Romell (1935) reported *Apheloria trimaculata* and *coriacea* (as *Fontaria*) extremely common in a humus layer of "super-crumb mull" 6 cm. deep. Much of this humus layer consisted of clumps of excrement made by the millipedes, and measuring from a few millimeters to several centimeters in diameter. These clumps were of essentially the same texture and composition as the soil surrounding them, both averaging 27% organic matter (loss on ignition), both containing "dead fragments of fungal hyphae and much other organic detritus, mixed with mineral granules." The most characteristic feature of the clumps was a large number of round imprints on one side, made by the rim of the anus, while on the opposite side the clump either mingled with the surrounding soil or, if separate, showed "a warty surface."

A few of the clumps were found to be hollow, with a smooth cavity inside, of a size to fit a rolled-up *Apheloria*. Romell inferred that these cavities might be "resting quarters dug out in old excrement clumps." According to my observations, reported below, they are "resting quarters," but not formed in that way. Romell's conclusions are significant: while this was an isolated case, it is clear that millipedes can be important in mixing organic and mineral matter, and that "earthworms have no monopoly on mull formation."

Apheloria in Peat at Rose, Wayne Co., N. Y.

Apheloria coriacea occurs in shady woods, usually under leaf litter or damp logs. The humus layer may be mull or mor; in the latter case, as shown by collected fecal material, they feed on organic matter with little or no mineral matter added. I have usually found individuals widely scattered and not abundant, and have noticed no difference between *coriacea* and *trimaculata* as to habits or habitat.

But in a deposit of woody peat one mile east of Rose, Wayne County, New York, Prof. E. V. Staker, R. F. Chandler, Jr., and the writer found altogether exceptional conditions. Most of the peat at this site is under cultivation and contains no *Apheloria*, but about an acre remains in virgin condition in a forest of large elm, beech, maple and other hardwoods. The

undergrowth on the peat is largely of annuals, such as jewel-weed, which dies down each fall, with a scattering of yew. In spring the water table stands within 8-10 inches of the surface, later dropping several feet. Earthworms averaged 90 per square yard in the upper six inches (not an unusual density); they were *Allolobophora caliginosa*, *Lumbricus rubellus* and *L. terrestris*, in that order of frequency. Mites, springtails and other minute arthropods occurred in numbers corresponding closely to their populations in rich forest humus layers (Eaton and Chandler, 1942).

In the upper six inches of woody peat the millipedes, *A. coriacea* and *A. trimaculata*, were present in great numbers, although not evenly distributed. The maximum concentration was roughly 40-50 per square yard, the majority being immature. Only in the adult and subadult stages can the two be separated; among these *coriacea* outnumbered *trimaculata* by about 4 to 1. Several individuals showed markings intermediate between the two, that is, with a narrow yellow band on each segment enlarged at the middle and at either side into spots. This suggests hybridizing.

The upper 6-8 inches of peat was loose, soft, moist and nearly black, with an organic content (loss on ignition) of 82-84%. From about 8-14 inches the material was more firmly compacted, so that large lumps taken out with a shovel readily held their shape. The texture was almost rubbery. In this layer no evidence of animals could be found, except a few earthworm burrows. Below this the profile consisted of several feet of reed and sedge peat, less decomposed than the woody layers since it was deposited in water and never exposed to the action of surface fauna and microflora.

Developmental Stages

On September 25, 1941, and March 16, 1942, the writer collected live specimens of *Apheloria* from the peat at Rose, New York, for laboratory study. The collections included all instars from the second (9 segments) to the eighth or adult (20 segments). Each instar, reached by an ecdysis or molt, shows distinctive characters, summarized in Table 1.

TABLE I

In- star	Length mm.	Av. wt. g.	Pig- ment	Sex	Pairs		Segments and number of pairs of legs																		
					Sex	legs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
I	1	.0001	no	M	3	..	1	1	1	?	?												
				F	3	..	1	1	1	?	?	?											
II	2	.0004	no	M	6	..	1	1	1	1	2	1										
				F	6	..	1	1	1	2	1											
III	3-4	.0011	no	M	11	..	1	1	1	1	2	2	2	2	2						
				F	11	..	1	1	1	2	2	2	2	2							
IV	5-5.5	.0045	no	M	16	..	1	1	1	1	2	2	1	2	2	2	2	2	2	2		
				F	17	..	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	
V	8.5-9.5	.0178	no	M	22	..	1	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2
				F	23	..	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
VI	14-17	.0842	trace	M	26	..	1	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	2	..
				F	27	..	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
VII	23-25	.3339	most	M	28	..	1	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	2	..
				F	29	..	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
VIII	30-45	.8771	full	M	30	..	1	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	2	..
				F	31	..	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

(A dash indicates a segment without legs. Sex difference in number of legs begins with the fourth instar.)

Figure 1 is a diagram of the segments and appendages of an adult male, showing that segments 1, 19 and 20 have no legs, 2, 3 and 4 have one pair each, and all the rest have two pairs each except the seventh, where the more anterior of the two is modified into a pair of clasping hooks or gonopods. In the female the 8th pair of legs occupies this position. Males of instars IV to VII have the gonopods represented by minute knobs. In Instar III the 8th pair of legs is present in all individuals, so that the sex cannot be distinguished, while in I and II the leg-series has not yet appeared so far back.

No specimens of instar I were found in these collections, but their characters may be inferred approximately from what is known of the hatching stage of other millipedes. Nearly all that have been observed show six segments (seven in *Euryurus*; Miley, 1927) and three pairs of legs (exception noted by Loomis, 1933, in *Arctobolus*).

The increase of length from one instar to the next is abrupt, with no transitions represented in the active specimens measured. This is because the ecdysis takes place in a prolonged resting period, when the animal is enclosed in a capsule. The same abrupt increment was found in weights. From one to ten

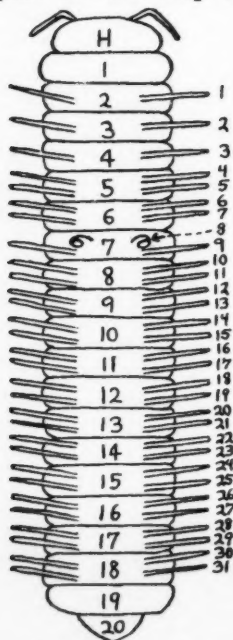


Fig. 1. Diagram of segments and appendages of adult male.

living millipedes of each instar provided the figures on length and weight. The quotients of weight increase (average of one instar divided by average of the preceding) averaged 3.69 (extremes 2.63 and 4.73), showing how great a change takes place, probably shortly after a transformed individual resumes feeding. In any one instar the maximum range of weight variation was 28% (among adults), and in the younger stages much less. A comparison of 5 adult males and 5 adult females (average .8871 g.) shows an average of .8074 g. for males (extremes .7474 and .9028) and .9468 g. for females (extremes .8305 and 1.0773). These animals had been feeding, so that the weight includes the contents of the intestine, but to starve them several hours in order to eliminate this would endanger them for later, more significant observations.

All the immature instars except VII are white, with a dark mid-dorsal line. This is probably correlated with the subterranean habit, for I have never seen any *Apheloria* but adults on the surface of the ground; the young are always, and adults frequently, below the surface. Examination of a living immature specimen shows that the dark mid-dorsal line pulsates. It indicates the dorsal blood vessel and its color is not from pigment or blood but is

the contents of the intestine visible through the blood vessel and the transparent dorsal wall. Fatty tissue and muscles form a white opaque layer inside the body wall except in the strip occupied by this vessel.

On or about May 15, 1942, one female laid 1076 eggs in a loose cluster among damp peat in a petri dish. Either they were infertile or conditions were unfavorable, for in six weeks none had hatched and mold was spreading on them. The color was yellowish buff, a few being dull red. They were spherical, smooth, and about .6 mm. in diameter. No special chamber was constructed, as reported for *Euryurus erythropygus* (Brandt) by Miley (1927) nor were any eggs encased in separate pellets as with *Arctobolus marginatus* (Say) (Loomis, 1933). Also the number was much greater in this case, compared with 586 for one female of *Euryurus* and 74 to 261 in *Arctobolus*. They were beneath the surface of the peat.

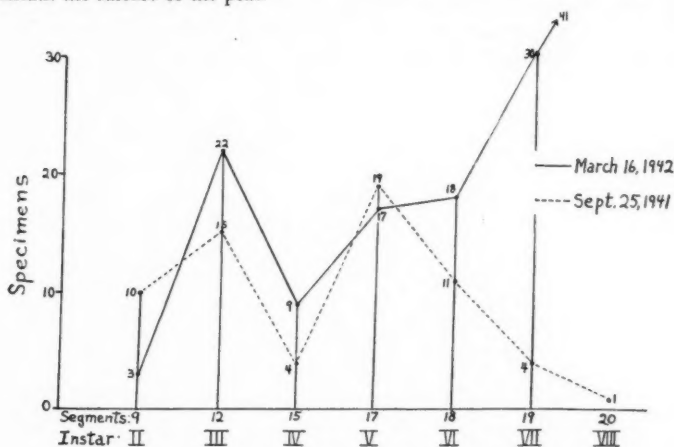


Fig. 2. Comparison of September and March collections.

Figure 2 gives a comparison of the September collection made at Rose, New York, with that of March. Specimens were taken at random with the exception of adults and subadults in the March lot. Two distinct peaks appear in both collections, one at the third and one at the fifth instar. The fact that no shift occurred in the position of the peaks is probably due to the winter temperature, retarding development between the two dates, although a tendency towards shifting is shown in the decline of stage II and increase of III in March. The partial segregation of these age-groups in the population may mean that the life-cycle at this latitude takes three years. Eggs laid in early summer might then develop to the third instar (except for a few stragglers in the second) by the end of that season. The second year would see most of this brood in the fifth instar by fall, while a third summer and winter would be required to produce adults.

Fecal pads, Capsules and Molting

Figure 3 shows a typical fecal pad produced by an adult in peat. These pads are emitted in an extremely wet condition, hence do not form separate pellets like the feces of most arthropods. The liquid drop is placed against whatever surface may be nearest to the animal's posterior end, and while the excess water is diffusing into the material of that surface, a few slight pushing movements are made. Then the animal abruptly draws away, having ensured that the pad will stick to the surface (usually previous pads) rather than to itself. In the pad is left a double imprint marking the everted rim of each side of the anus, which presses out the fecal material. From the size of this imprint one may recognize pads of individuals of different ages. The transverse diameter in the case of an adult is about 4 mm., the vertical 3.5 mm. Whether in peat, mull or other material, the appearance of the pads is essentially the same. As a rule the millipede feeds for some time in one place, so that a clump of pads gradually appears behind it.

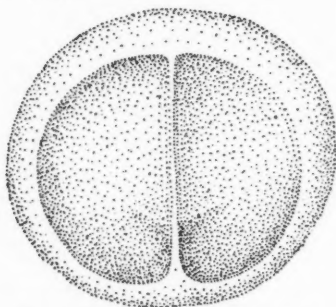


Fig. 3. Fecal pad of adult *Apheloria*.

The adaptability of such material to building capsules is obvious, for the fecal clumps become much more firm than the original food. In this study capsules like those observed by Romell were found in great abundance in the woody peat. A spadeful would contain several. A few were entire, with or without a millipede inside, but the majority were fragmentary. Often the interior was filled with a ball of excrement, showing that the millipede fed for some time with its posterior end still inside the capsule. Imprints on such a ball were larger than on the capsule itself, indicating growth of the animal since making the capsule.

In the natural peat, still retaining a high water content, the capsules were firm enough to withstand considerable pressure of the fingers. When dried in the laboratory they became extremely hard, so that a sharp blow was needed to break them.

In the following table the loss on ignition (organic matter) and resistance to crushing of the resulting ash are given for several *Apheloria* capsules (made by millipedes of stage VII) and for ground peat from the same site and level.

TABLE 2

	Capsules	Peat (ground)
Loss on Ignition:	83.923%	82.483%
	83.044	82.461
	82.931	
	83.236	82.472% average
	83.463	
	82.086	
	83.114% average	
Resistance to Crushing:	11.6 grams	0.56 grams
	(average of	(average of
	20 trials)	10 trials)

The crushing measurements were made by placing a capsule or portion of it (and similarly an undisturbed clump of ash from ground peat in a crucible) beneath the end of a carefully balanced rod, then adding, on this rod, weights taken from a chemical balance until a break was observed in the sample below. The results indicate that while there is no significant difference in the total organic content between the capsules and the surrounding peat (as in Romell's study on mull) yet a cohesiveness is found in the material of the capsules which persists to a high degree even in the ash. This must be the result of digestive action in the alimentary canal of the millipede, but the exact cause lies beyond the scope of this work.

Specimens of *Apheloria* kept in the laboratory were segregated according to instars, in petri dishes half filled with peat from a source not known to contain millipedes hitherto. They fed on it readily, and within a few weeks (April to June) the majority had built capsules. Capsules were not observed in the dishes of instars II and III, and I was not available. This should not be taken, however, as evidence that the early stages never make them. Construction of a capsule required several days. The millipede formed a cavity near but usually below the surface of the peat, depositing feces evenly around itself to make a smooth bowl-shaped wall. This it built higher and higher until only a small round opening appeared at the top. Finally this was sealed by the addition of a convex knob, like a pimple, particularly obvious in the smaller capsules.

The finished product was in most respects very similar to capsules made by *Euryurus* (Miley, 1927), even to the pimple. Apparently the walls made by *Euryurus* are thinner. The greatest difference is in the method of construction, for *Euryurus*, living in decaying wood, does not use feces at all. "Small bits of much decayed wood, or earth are moistened with a sticky fluid, presumably secreted by the salivary glands. The materials used are worked up with the jaws and front legs and when of a suitable size are placed together." This I have never seen *Apheloria* do.

When a finished capsule was opened the millipede would be found lying coiled on one side, usually motionless, but readily responding to the disturbance, and even crawling out again. After a number of days in the capsule,

however, it would reach a dormant phase, in which stimulation brought no response whatever. The following notes refer to a seventh-instar specimen in this condition:

Lies tightly coiled on side with head in center. Skin very soft except dorsally. Appears partly distended with molting fluid beneath. Looks more translucent than usual. Legs, head and last three segments of body especially glassy. Legs lie back against each other. Spiracles show clearly above base of each leg, because edged with white.

The process of ecdysis has not been observed, but freshly molted specimens are soft, sluggish, and (even in the adult and subadult for a few days) have little or no pigment. During the dormant and later period the body wall is flexible enough to accommodate an increased bulk. No complete shed skin was found, but often separate fragments from the legs and other parts, suggesting that the animal may eat most of it.

Feeding

In order to learn the part which these millipedes may play in the formation of humus material in forests, I made several feeding tests. Pairs of adults were first put in petri dishes on wet absorbent paper and left 24 hours without food.

Clean dead leaves of basswood, sugar maple, white ash, white oak and beech were soaked one hour in a minimum amount of water and then supplied to the millipedes. 48 hours later the animals were not feeding and gave no evidence of having fed. In each alternate dish I then put about 3 cc. of fresh peat. In ten minutes more than half of the millipedes were eating the peat. The following day the remainder were also fed, with the same result. This seems to show that undecomposed dead leaves, even when softened by wetting, are not edible.

Two pairs of adults originally from peat were placed in petri dishes of mull soil taken from nearby deciduous woods, with no leaves or other free organic material. For three weeks, as long as they were left there, they fed freely on the mull.

Three specimens were enclosed in a dish with a piece of much softened dead bark of white oak, previously fed on by millipedes of another genus, *Parajulus*. The *Apheloria*s did not refuse, but ate sparingly of the softest part.

Finally they were changed to a dish containing an accumulation of feces of *Parajulus* (from the same source) and these they ate.

During the whole study woody peat was the staple diet for the whole stock of *Apheloria*. In some cases they would use the same material over and over, where the amount was small in proportion to the number of animals. From observations in the field I think they do this normally when pressure of population requires it, and that mites, springtails and many other soil arthropods feed largely on arthropod fecal matter. This will be reported elsewhere in more detail.

The conclusion by Romell (1935) that *Apheloria* (*Fontaria*) forms mull requires certain qualifications. Mull already formed may be used as food and

so continue as mull. An *Apheloria* feeding on largely decomposed organic matter of a mor humus layer, or in a decayed log, just over mineral soil, may happen to feed also on the mineral soil, thus adding it to the organic matter and forming mull. If located where mineral soil is not available, however, as in the woody peat deposit, its feeding will not produce anything definable as mull. This animal has no behavior comparable to that of an earthworm pulling dead leaves into the ground and consuming them along with the soil in which it lives.

Casual Activity

In comparison with certain other millipedes, for example *Parajulus pennsylvanicus*, *A. coriacea* is sluggish, moving less frequently and (relative to its size) less rapidly. To obtain some measure of the amount of this casual activity I made a total of 900 observations on 20 segregated pairs of adults. Pairs 1-10 were in moist peat in petri dishes, where they had been established for more than a month, one pair per dish. The observations were made on April 17, 18 and 21. At the same time pairs 11-20 were placed in petri dishes without peat, but on moist paper only. Observations on these were made April 17 (five hours without food) and April 18 (23 hours without food). On the 20th these (pairs 11-20) were supplied again with peat, and the third set of observations made on the 21st.

The temperature during the observations was 27.4° C. on the 17th, 24.6° on the 18th, and 24.5° on the 21st. Each time the procedure was to record, at 5-minute intervals, 15 times, the amount of movement seen in a brief glance, and to evaluate it arbitrarily. If an animal were motionless the record was 0; if a part of the body or appendages moved, it was noted as 1; and if the whole millipede were moving, it was 2. Thus for a given pair one record might be either 0-0, 0-1, 0-2, 1-1, 1-2 or 2-2. For the whole series of 15 records for a pair the sum of the figures might be anything between 0 (no motion of either) and 60 (both moving actively all 15 times). Actually the range was from 0 to 42.

It was not possible under these conditions to record the sum of movement of a single individual, but only of the pair. Also in some cases there was mutual stimulation, as when one crawled over the other, previously resting, and started it moving. Care was taken, however, not to disturb the animals before or during the period. They are blind. Each time they were observed under moderate artificial light.

Pairs 1-10 in peat gave the following results. Average activity per 15 observations:

April 17: 8.1 per pair (4.05 per individual)
April 18: 7.3 per pair (3.65 per individual)
April 21: 8.3 per pair (4.15 per individual)

Particular pairs sometimes showed consistent amounts through the three days, e.g.,

Pair 4: 0, 3, 6.
Pair 8: 2, 0, 4.
Pair 6: 16, 14, 25.
Pair 9: 13, 10, 10.

This, with the previous figures, suggests that the casual activity of these animals under approximately natural conditions, while variable individually, is low. That is, it averages about 10-15% of the maximum possible under continuous stimulation. For higher temperatures more might be expected. Movement declines at lower temperatures but does not stop entirely until the air is close to 0° C.

Pairs 11-20 (two days without food, third day with food) showed the following results:

April 17: 15.9 per pair (7.95 per individual)

April 18: 11.9 per pair (5.95 per individual)

April 21: 9.5 per pair (4.75 per individual)

On the foodless days the activity was above normal, the second day declining somewhat, probably on account of loss of energy from hunger. On the third day, after 24 hours with food, the activity was approximately that of pairs 1-10.

It would be advisable to extend this kind of observation further, to include especially (a) the activity of isolated individuals, (b) activity through a considerable range of temperature, (c) activity in darkness and maximum daylight, (d) activity at different periods of the 24 hours, (e) comparison with other species and genera.

Mating Behavior

The more important phases of behavior of the adult *Apheloria coriacea* seem to be these: resting, wandering, feeding, grooming, mating. In common with most other arthropods they clean their antennae, legs and accessible parts of the body by nibbling off particles of soil or other foreign objects, particularly when they have just been placed in a new situation. I have noticed 13 out of 20 specimens grooming themselves simultaneously soon after being put in dishes of fresh peat.

Mating behavior, observed several times, is initiated by the male climbing on the back of the female and crawling along until his head is over and a little in front of hers. He then bends his head down to one side, attempting to get it beneath the female's head, while retaining hold dorsally with the posterior part of his body. On two occasions a male was seen to crawl the wrong direction on the female, discovering and correcting his mistake after reaching the posterior end. Having no eyes, these millipedes must depend on tactile and possibly chemical senses to detect the features and responses of the opposite sex. When the male is in position with his head down against the female's, she responds in most cases by avoidance, that is, jerking her head still lower, making it impossible for the male to get underneath. After a minute or two in this position she will try to withdraw, moving backwards and sometimes jerking, until the male leaves.

If the response is favorable, the male's head comes underneath, forcing the female to raise her anterior end, and about the first third of the bodies of both lie parallel, venter to venter, while the male keeps his dorsal position behind.

The reason for this anterior contact, of course, is that in millipedes the openings of the reproductive ducts are on the second segment, not at the posterior end. The more anterior legs of the male are now extremely active, holding and releasing continually, while his head remains bent against the front of hers, a little in advance. When the gonopods take hold, both individuals usually become quiet, but not always. The male's legs may continue their activity, or the gonopods may be withdrawn and thrust in again. Apparently this depends on the success of mechanical adjustment. In one case, after a moment of quiescence, the female began to back away but the male held on. In a few seconds drops of liquid appeared at the pores of the stink glands of the female. These are located on the lateral keels of segments 5, 7, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19. She pulled and bent until the male let go.

In the few apparently successful cases observed copulation lasted only two to three minutes, and was ended by the female becoming restless, pulling backward, and then crawling away, sometimes over the supine and quiescent male. This contrasts with casual observations of *Parajulus pennsylvanicus* and *Polydesmus serratus*, in which it lasts much longer.

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Acanthocephalus van-cleavei, a New Echinorhynchid Worm, from a Salamander*

R. Chester Hughes and George A. Moore

Ten out of 73 specimens of *Eurycea tynerensis* Moore and Hughes 1939, a neotenic plethodontid salamander, collected from Pea Vine Creek, a tributary of the Illinois River some 13 miles north-northeast of Tahlequah, Oklahoma, in April, May, and June 1942, were found to be infected with an apparently new spiny-headed worm for which we propose the name *Acanthocephalus van-cleavei*. A total of 15 examples (1 male and 14 females) were obtained, 3 being the maximum number from a single host.

Following suggestions of Lynch (1936) some of the worms were immobilized in 10 per cent alcohol, fixed in Carnoy and Lebrun's fluid, and stained with borax carmine. Dehydration and clearing were effected very gradually and the specimens were studied as temporary mounts in the clearing agent (beechwood creosote) on hanging drop slides. Beautiful preparations, with fully extended proboscides and free from any trace of distortion, were thus obtained; further, by sliding the cover glass, the animals (especially the male) could be shifted about and viewed from various angles. At the conclusion of the study permanent Clarite mounts of the worms were made.

Acanthocephalus van-cleavei sp. nov.

(Plates 1 and 2)

Female.—Description based on 14 specimens. Body, exclusive of proboscis, 4.66 (3.05-6.7) mm. long and 470 (330-700) μ wide; nearly uniformly cylindrical with rounded ends—sometimes slightly enlarged anteriorly. Proboscis 218 (147-267) μ long and 159 (90-220) μ in diameter; armed with 14 to 19 rows of hooks having sometimes 5 spines each, sometimes 6 each, sometimes 5 and 6 alternately. Designated according to the scheme of Van Cleave (1915) in which the hooks in the more forward-pointing rows are numbered, from the tip posteriad, 1, 3, 5, 7, etc., and those in adjacent rows 2, 4, 6, 8, etc., the external portions of spines 1 to 10 of one specimen measured respectively 45, 67, 78, 97, 97, 105, 84, 75, 66, and 45 μ in length; those of another 43, 50, 54, 57, 58, 58, 50, 36, 35, and 30 μ . Proboscis receptacle 393 (200-600) μ long and 144 (90-233) μ in diameter. Lemnisci subequal; 2 to several times as long as proboscis receptacle; the longer 1251 (666-1760) and the shorter 1071 (367-1692) μ long; generally one, and in one case both, branched—the position of the forking and the relative sizes of the two prongs being markedly variable. In one case the rami of a bifurcate lemniscus are approxi-

* Contribution No. 109 from the Department of Zoology, Oklahoma Agricultural and Mechanical College.

mately equal and the structure is double for most of its length; more often one of the branches appears as a small bud-like protuberance on the other. Genital tract inclusive of uterine bell and vagina 465, 512, and 600 μ long severally in 3 specimens. Eggs 54-72 x 12-18 μ .

Male.—Only one specimen at hand. Body, exclusive of proboscis and copulatory bursa, 4.3 x 0.4 mm. Proboscis 240 x 135 μ . Hooks in 14 rows comprising alternately 5 and 4 spines each; similar in shape and size to those of females. Proboscis receptacle 400 x 133 μ . Lemnisci very unequal in size and form; the smaller diminutive, unbranched, and 150 μ long; the larger 5-branched and 1584 μ long to tip of longest ramus. Testicular field 1644 x 120 μ —boundary between testes not clearly observed. Vasa efferentia plainly visible—the dextral with 4 and the sinistral with 3 seminal vesicles. Vas deferens with 1 seminal vesicle. Cement glands 7 in number, comprising 3 pairs with single ducts and a median example with a pair of ducts. Extruded bursa 413 μ long and 276 μ wide at distal extremity.

Host.—*Eurycea tynerensis* Moore and Hughes 1939.

Incidence.—About 13.7 per cent of 73 salamanders examined especially for this worm were infected.

Locality.—Pea Vine Creek, a tributary of the Illinois River, near Tahlequah, Cherokee County, Oklahoma.

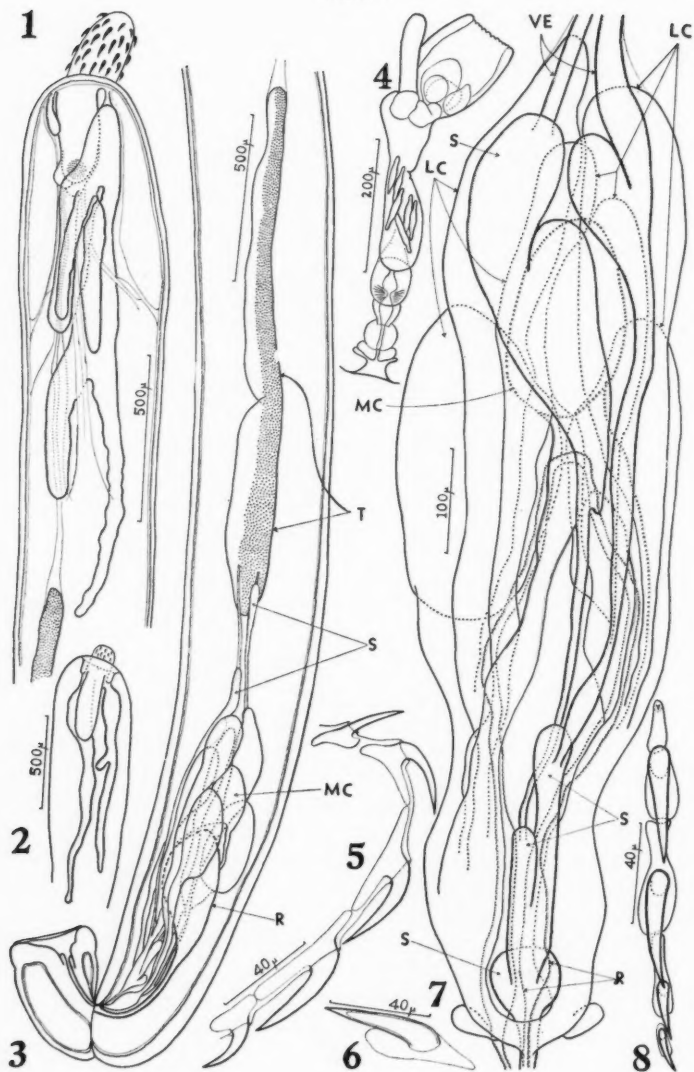
Cotype Specimens.—*In toto* mounts of 3 females and 1 male in the United States National Museum.

Discussion.—The genus *Acanthocephalus* Koelreuter 1771 embraces some 25 previously described worms parasitic as adults in fish and Amphibia. The new species was studied in comparison with descriptive data on all of the earlier batrachian forms—our sources of information being the compilatory accounts of Meyer (1932) for the older species and the original descriptions of Van Cleave (1925, 1931a, and 1937) for the newer ones.

The previously known amphibian species of *Acanthocephalus*, listed herewith, differ from *A. van-cleavei* sp. nov. as severally indicated:

- (1) *A. acutulus* Van Cleave 1931 from *Triturus* in North Carolina is somewhat larger with larger proboscis and smaller and more numerous hooks;
- (2) *A. anthuris* (Dujardin 1845) Lühe 1911 from Caudata in Europe is larger in both sexes and has a larger proboscis, much more numerous hooks, relatively shorter lemnisci, and egg-shaped testes;
- (3) *A. artatus* Van Cleave 1925 from *Rana* in Japan is much larger;
- (4) *A. bufonis* (Shipley 1903) Southwell and MacFie 1925 from *Bufo* in Hongkong has a much larger body in both sexes, a much larger

PLATE I



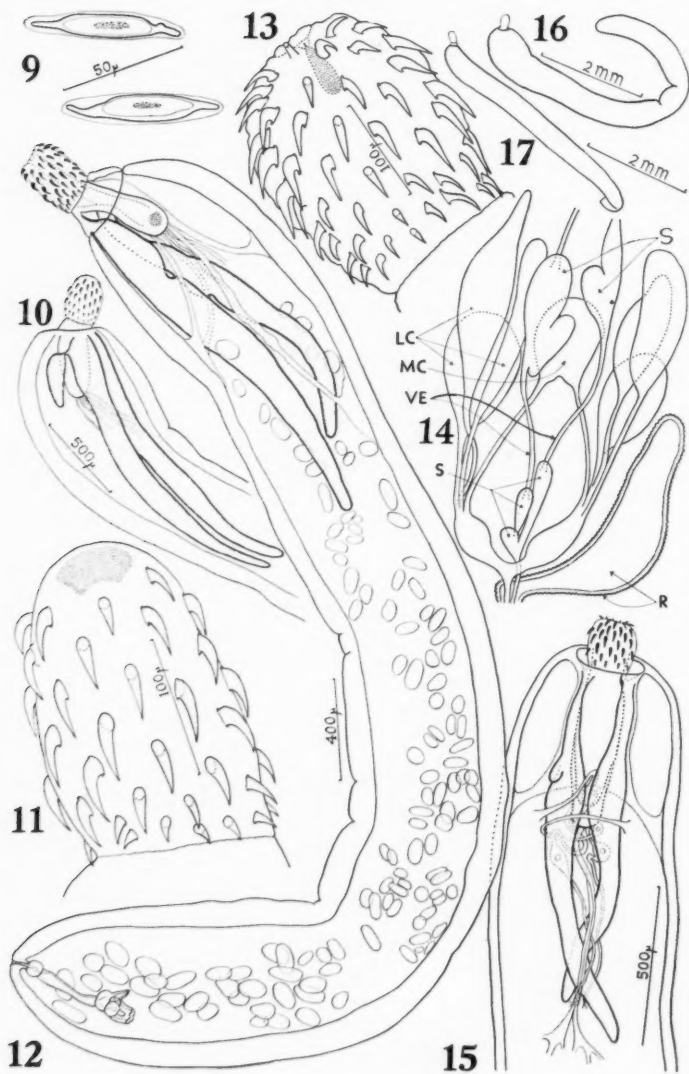
proboscis receptacle, somewhat more numerous hooks, and relatively much broader eggs;

- (5) *A. elongatus* Van Cleave 1937 from *Bufo* in China has the proboscis actually and relatively much larger and the hooks more numerous per row;
- (6) *A. falcatus* (Froelich 1789) Lühe 1911 from *Salamandra* in Europe is a much larger worm;
- (7) *A. lucidus* Van Cleave 1925 from *Rana* in Japan has a larger body in the female, a larger proboscis in the male, relatively smaller lemnisci, and much larger embryos;
- (8) *A. lutzii* (Hamann 1891) nobis from *Anura* in South America has the body larger and more plump in both sexes, testes broadly ovoidal, embryonated eggs relatively broader, and "Zementdrüsen 4 (!)";
- (9) *A. nanus* Van Cleave 1925 from *Diemictylus* in Japan is much larger in both sexes with larger and more slenderly elongate proboscides, relatively smaller hooks in fewer rows, and relatively smaller lemnisci;
- (10) *A. ranae* (Schrank 1788) Lühe 1911 from *Anura* and *Caudata* in Europe and (Van Cleave 1915) from *Triturus* in Maryland has the body in both sexes, the proboscis, and the proboscis receptacle all much larger, the lemnisci relatively much smaller, and the eggs longer and relatively more slender; and
- (11) *A. sinensis* Van Cleave 1937 from *Anura* in China is larger in both sexes with somewhat larger hooks and somewhat smaller embryos.

Noteworthy features of the new species include (a) the exceptionally elongate and frequently branched form of the female lemnisci, (b) the marked

PLATES 1 AND 2. All figures concern *Acanthocephalus van-cleavei* sp. nov. and, except Nos. 14, 16 and 17, were made with the aid of a *camera lucida*. Lettering: *lc*, lateral (paired) cement glands; *mc*, median (unpaired) cement gland; *r*, receptacle of bursa copulatrix; *s*, seminal vesicle (*s*); *t*, testes; *ve*, vasa efferentia. Figs. 1-17: 1. Anterior end of male. Note that one lemniscus is diminutive and the other 5-branched.—2. A rather typical pair of lemnisci—from a female.—3. Posterior end of the male represented in Fig. 1.—4. Female genital tract including uterine bell and vagina. Note eggs *in utero*.—5. A row of proboscis hooks, side view.—6. A single hook, oblique view.—7. Cement glands and associated structures of the male. The median gland and its two ducts are represented in double outline. See Fig. 14.—8. A row of proboscis hooks seen from above. Figs. 5, 6, and 8 were all made from the same worm.—9. Two eggs.—10. Another pair of lemnisci. Note that one has a narrowly stipitate branch.—11. Proboscis of the male.—12. Female—fewer than half of the total number of ovarian balls observed in the worm are represented.—13. Proboscis of a female.—14. A free-hand schematic representation of the principal features shown in Fig. 7.—15. Anterior end of a female.—16. A large female the body cavity of which was almost completely filled with ovarian balls and eggs. Sketch made with a projection apparatus.—17. Projection-apparatus sketch of the male.

PLATE 2



dissimilarity in size and form of the male lemnisci, (c) the slenderly elongate form of the testes, and (d) the occurrence of 7 cement glands. The one male which we possess may be anomalous with regard to the three features last mentioned. Members of the family Echinorhynchidae Cobbold 1879, to which *Acanthocephalus* belongs, "regularly possess six well defined cement glands" (Van Cleave 1931b). Should 7 prove to be its normal number of prostatic glands the new species may perhaps deserve recognition as representing a new genus.

According to Meyer (1932) *A. falcatus* "ist möglicherweise oder wahrscheinlich identisch mit" *A. ranae*. Harada (1935) considers *A. lucidus* to be identical to *A. artatus*.

Acanthocephala are comparatively rare in Amphibia. In his host catalogue for spiny-headed worms Meyer (1933) lists only species of *Acanthocephalus* as having been found to occur normally in adult form in hosts of this class. It may be noted that of the species mentioned above only *A. acutulus*, *A. ranae*, and *A. van-cleavei* have been reported from North America.

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Studies on Monogenetic Trematodes

IX. Host Specificity of *Pomoxis Tetraonchinae**

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In 1938 the senior author observed four species of *Tetraonchinae* as gill parasites of black and white crappies (*Pomoxis nigro-maculatus* and *P. annularis*, resp.). It seemed very striking that of the four species, specimens of only two, viz., *Cleidodiscus vancleavei* and *C. capax*, were found in the black crappie (*P. nigro-maculatus*), whereas all four of the species, viz., *C. vancleavei*, *C. capax*, *C. longus*, and *C. uniformis* were recovered with great regularity from the gills of the white crappie (*P. annularis*). The possibility concerning the confusion of host identification was assumed to be nil since Drs. D. H. Thompson and D. F. Hansen of the Illinois State Natural History Survey, both of whom are ichthyologists, determined the species in all instances in which there was any doubt.

In 1936, Mueller described *Onchocleidus formosus* from the gills of black crappies taken from Lake Okeechobee at Clewiston, Florida. This species was later (Mizelle 1938) shown to be a synonym of *C. vancleavei* Mizelle, 1936. In 1937 (a) Mueller reported specimens of *C. capax* from black crappies taken from Oneida Lake, New York, and Lakeland, Maryland. So far as the present authors are aware, Mueller has never reported gill parasites from the white crappie and neither has he reported recovery of either *C. longus* or *C. uniformis* from any host. In 1937 however, in a list of parasites for several species of fishes, he gave the four above-named valid species and also *O. formosus* for both crappies. The same information was again given in a subsequent publication (Mueller 1937a) and an appended note stated, "Because of possible confusion in the determination of the host, the exact host selection of some of these species is not known."

The senior author of the present paper became interested in whether or not all four species of the *Tetraonchinae* in question might infrequently occur on the gills of the black crappe as well as on those of the white crappie, and steps were taken to find out the true status of the situation.

In 1941, O'Shaughnessy examined 64 specimens of *Tetraonchinae* which were recovered from black crappies taken from Reelfoot Lake, Ridgely, Tennessee, by Dr. Carl Venard (Ohio State University, Columbus, Ohio) and kindly sent them to the senior author. Of these 64 parasites, 58 were specimens of *C. vancleavei* and 6 were *C. capax*. Sometime later Dr. R. V. Bangham (College of Wooster, Wooster, Ohio) sent the senior author a vial of material

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from the gills of white crappies taken from the same place. Examination revealed 21 specimens of *C. vancleavei* and 1 of *C. uniformis*. Obviously, these data supported the findings of Mizelle (1938) concerning host specificity of crappie *Tetraodonchinae*.

To further substantiate previous conclusions, Dr. Venard was contacted to make arrangements for shipment of several black and white crappies from Reelfoot Lake for additional data. Upon receipt of these specimens, the gill material was treated in the usual way (Mizelle 1938) and the parasites were mounted in glycerine for examination. A total of 134 parasites was recovered from two black crappies; of these 133 specimens belonged to *C. vancleavei* and one belonged to *C. capax*. In the examination of 10 white crappies 458 specimens of *Tetraodonchinae* were recovered. These included 236 specimens of *C. longus*, 185 of *C. vancleavei*, 34 of *C. uniformis*, and 3 of *C. capax*. It is regrettable that more specimens of *P. nigro-maculatus* were not available. However, there seems to be enough information from the above and previous data (Mizelle 1938) to conclude safely that only two (*C. vancleavei* and *C. capax*) of the four species of *Tetraodonchinae* which infest the gills of the white crappie occur on the gills of the black crappie.

As a matter of fact, the senior author of the present publication is of the opinion that *P. nigro-maculatus* and *P. annularis* may be separated by the presence of gill parasites as well as by structural characteristics. Since this publication went to press the authors have examined three black crappies and two white crappies kindly supplied from the Mississippi River in Illinois by Dr. D. H. Thompson of the Illinois State Natural History Survey. Data from these hosts are in accordance with the above findings.

The authors are grateful to Dr. Carl Venard who supplied material directly and arranged for shipment of fish from Tennessee; to Dr. R. V. Bangham, who contributed the Reelfoot Lake material he collected; to Dr. C. L. Baker of the Reelfoot Lake Biological Station for his generous cooperation in procurement of host species; to the Tennessee Academy of Science, which aided Dr. Venard's activities by means of a grant; and to Dr. D. H. Thompson of the Illinois State Natural History Survey who also supplied host species for examination.

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Siliceous Sponge Spicules from the Lower Pennsylvanian of Montana

Harold W. Scott

"It is needless to dilate on the limitations imposed on one who undertakes to describe a collection of sponges," wrote Dr. H. V. Wilson, foremost authority on modern sponges, forty years ago when he described a collection from Porto Rico. The statement is equally true concerning the difficulties confronting the paleontologist who attempts to describe a group of fossil sponge spicules; indeed, the limitations are multiplied many fold. There are only a few papers describing sponge spicules from North America and this has led some workers to believe that spicules of Paleozoic age are rare. The apparent paucity, however, may be partially explained by the difficulties of classification.

During the course of micropaleontological examination of a suite of Montana Quadrant siliceous limestones, a diversified sponge spicule assemblage was discovered. The spicules were obtained from the Quadrant section exposed in the south wall of the canyon of the Jefferson River, twenty miles west of Three Forks, and about two miles east of LaHood Park along U. S. Highway No. 10. At this place the Paleozoic strata dip about 45 degrees west and the Quadrant is composed for the most part of quartzite interbedded with thin arenaceous limestones. The spicules occur in the calcareous centers of irregularly shaped gray chert lenses and nodules. The chert is interspersed through an arenaceous limestone.

The siliceous spicules are readily recognizable in the field without the aid of a hand-lens and they are easily obtained from the matrix by dissolving in cold dilute hydrochloric acid. Great difficulty, however, is encountered in separating the individual spicules from the dried residue, because the large number of individuals and great variation in shape results in an interwoven mass that does not readily part. This may be partially overcome by allowing very small residues to accumulate and by touching inter-twined spicules with a moist brush.

Ordinarily, outline drawings are sufficient to show the characteristics of simple sponge spicules. Some of the Quadrant spicules could not be adequately represented by that method, and therefore, the writer painted all forms on a black background by using reproduction white and lamp black paints.

The writer is pleased to acknowledge the valuable criticisms made by Dr. A. H. Sutton, University of Illinois. Special mention is made of the many important publications on modern sponges by Dr. H. V. Wilson, Professor of Biology in the University of North Carolina.

Modern and Fossil Sponge Spicules

The skeleton of a siliceous sponge is made up of spicules of various shapes. The spicules have a central axial canal which cannot always be observed in the fossil state. Sponges are among the most plastic of organisms and considerable variation is observed among individuals of the same species. Variation phenomena force themselves upon the zoologist interested in taxonomy of sponges and greatly hinder practical classification. In fact, these variations are described but to a great extent disregarded insofar as assigning individuals to definite categories.

Isolated modern spicules cannot be correctly classified generically unless some unusual characteristics are present. In fact, most spicules cannot be relegated to their proper families and in most cases the oxeate types cannot be placed in the correct suborder. This condition has long been a recognized fact among students of modern sponges, and therefore, they have adopted the admirable habit of giving all spicules of similar architectural design a form name. It is practically impossible to distinguish between the streptasters or microxeas of the modern *Characella* and *Poecillastra*. This similarity between spicules of different genera in conjunction with the great diversity of form exhibited in the spicules of one species makes biological classification impossible on the basis of spicules alone (see Fig. 1). Many other examples of similarity

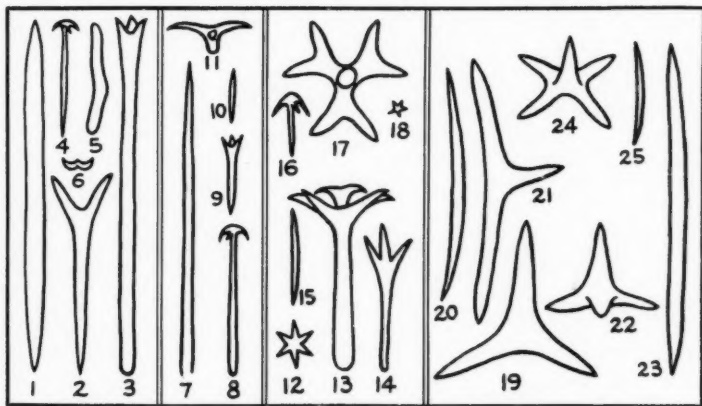


Fig. 1. Spicules from four genera of sponges.—1-6. *Tetilla* (*Cinachyrella*) *crustata* Wilson. 1, oxeate; 2, prodiaene; 3, protriaene; 4, anatriaene; 5, promonaene; 6, sigma.—7-11. *Paratetilla arcifera* Wilson. 7, oxeate; 8, orthotriaene; 9, protriaene; 10, small oxeate; 11, anatriaene.—12-18. *Geodia philippinensis* Wilson. 12, choansomal oxyaster; 13, dichotriaene; 14, protriaene; 15, oxeate; 16, protriaene; 17, cladome of a dichotriaene; 18, dermal oxyaster.—19-25. *Dercitopsis minor* Dendy. 19, triode; 20, 23, oxeates; 21, orthodiaene? 22, tetractine; 24, pentact; 25, microxeate.—*Tetilla* and *Paratetilla* belong to the suborder Sigmatophora, *Geodia* to Astrophora, and *Dercitopsis* to Homosclerophora. Note similarity of spicules between suborders and variety of spicules within one species.

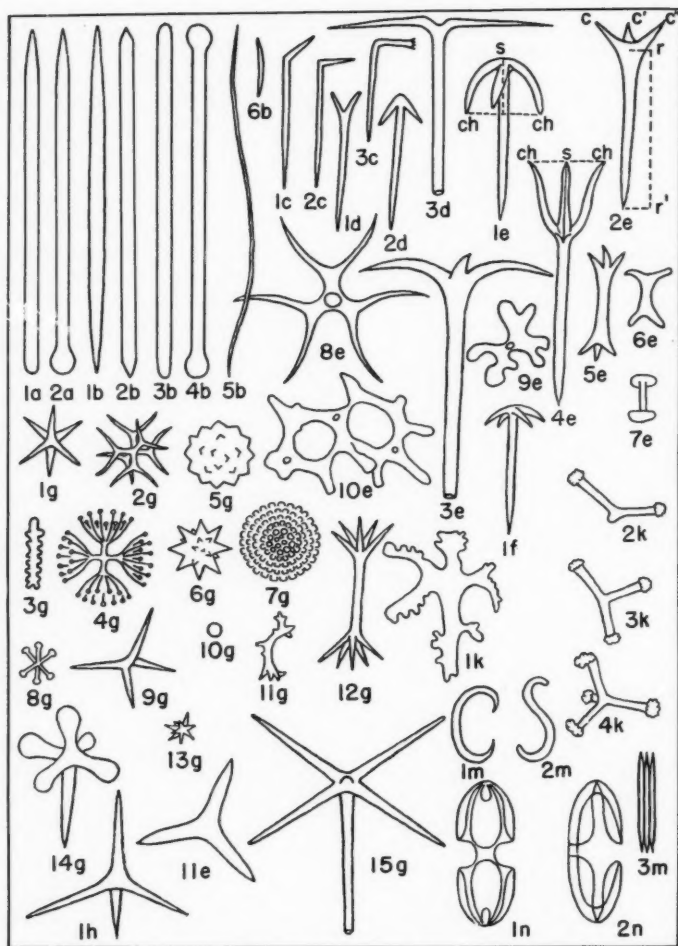


PLATE 1.—Diagrams representing the commonest types of sponge spicules. Figs. 1a, 2a. *Monactines*. 1a, style; 2a, tylostylus. 1b-6b. *Diactines*. 1b, oxea; 2b, tornote; 3b, strongyle; 4b, tylole; 5b, raphide; 6b, microxea. 1c-3c. *Monaenes*. 1c, promonaene; 2c, orthomonaene; 3c, dichomonaene. 1d-3d. *Diaenes*. 1d, prodiaene; 2d, anadiaene; 3d, orthodiaene. 1e-11e. *Triaenes*. 1e, anatriaene (ch, chord; s, sagitta, perpendicular distance from chord to cladome); 2e, plagiotriaene (c, c', c'', cladi. The cladi together constitute the cladome. rr', shaft or rhabdome); 3e, orthotriaene; 4e, prototriaene (ch, chord; s, sagitta); 5e, amphitriaene; 6e, amphidaene; 7e, amphidiscus; 8e, dichotri-

could be cited. In fact, the writer finds it impossible to distinguish between many Paleozoic spicules and modern forms.

Howell and Landes (1936) point out an important spicule association; viz., simple oxeas occur in great numbers in the order *Tetraxonida* associated with four-rayed sclerites. If such an association is found, there is no basis for classifying the oxeas under *Monactinellida*. This problem is further discussed under remarks on oxeas in this report.

Because of the similarity between fossil and modern spicules and the close relationship in form between modern genera, it is believed inadvisable to base a fossil generic name on a modern genus by adding "ites," as has occasionally been done. To call a certain Paleozoic sterraster *Characellites* would indicate relationship with the modern genus *Characella*, though actually it might be as closely related to several other genera. Furthermore, it very possibly would have no relationship to *Characella*, and might not even belong to the same family. But the most confusing of all methods has been the placing of various forms such as oxeas, oxyasters, and plagiostrophiae in one species and then attempting to place slightly different specimens of the same forms in another species or genus.

It seems impossible ever to arrive at a satisfactory basis for classifying fossil spicules. To assign them to genera and species is a travesty upon our accepted ideas of the construction and evolution of organisms and upon our knowledge of the construction of modern sponges. From the standpoint of spicule shape the fossil genera, as previously used, included many different architectural forms that undoubtedly bore no genetic relationship to each other. Past methods of classification not only lead to erroneous conclusions regarding the development and relationship of fossil and modern sponges, but also confuses the taxonomist. Furthermore, the classification has made spicules of little, if any, stratigraphic value.

In order that the fossil spicule may be of more value in tracing the history of modern forms and in stratigraphic use, the writer here adopts the sponge spicule form name used in describing modern sponges and, therefore, does not assign them to genera and species. My first attempts at classification of spicules were along the binomial system of nomenclature, but it was soon realized that such diverse forms as those which have been described as *Hexactinellida delicatula*, *Reniera siliqua*, and *Geodites pateus* might have belonged to the same animal. Because a true biological method was utterly impossible an artificial "form" classification was attempted. The method consisted of forming generic

ane; 9e, gastral phyllotriaene; 10e, dermal phyllotriaene; 11e, triode. 1f, lh, *Tetroenes*. 1f, anatetraene; 1h, tetractine (calthrops). 1g-15g, *Asters*. 1g, oxyaster; 2g, oxyhexaster; 3g, sanidaster; 4g, sphaerohexaster; 5g and 6g, two forms of sphaerasters; 7g, sterraster; 8g, chiaster; 9g, metaster; 10g, spherule; 11g, spiraster; 12g, amphiasster; 13g, streptaster; 14g, tylaster?; 15g, pentact. 1k-4k, *Desmas*. 1k, monocrepsis; 2k, dicrepis; 3k, tricrepis; 4k, tetracrepsis. 1m-3m; 1n, 2n, *Microscleres*. 1m, sigma; 2m, sigma-spire; 3m, trichodragmata; 1n, chela, face-view; 2n, chela, side view.

names by changing such descriptive terms as anatetraene to *Anatetraenites*, orthotriaene to *Orthotriaenites*, etc.

Although this system is probably the best artificial classification possible and has a distinct advantage over the method used by Howell and Landes, viz., calling certain fossil oxeas *Petrosites* after the modern genus *Petrosia*, it nevertheless had the unfortunate distinction of being artificial. This method was suggested in 1936. Further study has shown the possibility of a slightly different method, not entirely satisfactory, which avoids the erection of many new genera. It also avoids the inclusion of differently shaped spicules in the same genus as well as identically shaped spicules in different genera. It involves describing them under the biological structural name and lettering the different types. The advantages of such a system are quite apparent. In the first place, the types are not species and are not so named; second, the groups are neither artificial nor real genera; third, the group names are biological types and will ultimately furnish us with information concerning the development of the sponge skeleton; and finally, they can be assigned to definite groups and therefore may be used for stratigraphic purposes. Of course, this plan may be criticized as not being a classification at all, but at this time it appears to be the most satisfactory method of studying a very diverse and plastic group of fossils.

In general, paleontologists have not used the form name for different kinds of spicules. The names are so usable for descriptive purposes and so well established in zoological literature that it seems apropos to introduce them. Only the most common types are given. The definitions used are mostly after Wilson, Delage and Hérouard, though some are slightly modified by the writer in order to make them more usable in describing fossil spicules. No attempt is made to list all of the descriptive terms.

Definition of Systematic Terms Used

Actine. The ray of a uniaxial (diactinal or monactinal) spicule or of an aster.

Amphidiaene. A shaft bearing two clads on each end. Fig. 6e.

Amphidiscus. A shaft, usually short, bearing a round disc at each end. Fig. 7e.

Amphitriaene. A shaft bearing three clads on each end. Fig. 5e.

Anadiaene. A monaxon in which the two clads are directed backward, making an acute angle with the rhabdome. Fig. 2d.

Anatetraene. A monaxon with four clads directed backward. Fig. 1f.

Anatriaene. A triaene in which the clads are directed backward. Fig. 1e.

Aster. A microclere in which several rays (actines) proceed from a center or from a longer or shorter axis.

Centrum. Point of juncture of two or more actines.

Chela. A microclere consisting of a more or less curved axial part, the shaft bearing at each end several recurved processes, the teeth. Figs. 1n and 2n.

Chiaster. A minute aster with very slender cylindrical rays, knobbed or not, sometimes truncate, at the ends. Fig. 8g.

Chord. Distance between the ends of two clads. Figs. 1e and 4e.

Cladome. Point where clads spring from the rhabdome.

Clads. The rays at the end of a shaft or rhabdome. Fig. 2e.

Desma. An irregular, gnarled spicule. Figs. 1k, 2k, 3k, and 4k.

Deuterocladus. The distal divisions of a dichotriaene.

Diactinal. Term applied to a uniaxial spicule in which growth proceeds in opposite directions from the point of origin. Thus, two equivalent and usually similar rays (halves) are produced, the point of origin remaining at or near the middle of the spicule.

Dichomonaene. A monaxon which possesses a clad that is bifurcated. Fig. 3c.

Dichotriaene. A triaene in which the cladi are dichotomously divided. The undivided part of the cladus is the protocladus. The distal divisions are the deuterocladi. Fig. 8e.

Dicrepis. A desma with two actines. Fig. 2k.

Ecactine. The centrifugal part of a radially arranged rhabdus.

Euaster. Comprehensive term applied to asters in which the rays proceed from a center and not from an axis.

Hexact. Six rayed spicules, the actines meet at a common center. Fig. 1g.

Isoactinate. When both actines of a diactinal spicule are alike in shape and size, the spicule is said to be isoactinate.

Isochela. A chela in which the two ends are alike and equal.

Megasclere. One of the larger spicules which compose the supporting skeleton.

Microsclere. One of the small spicules scattered irregularly through the body in many sponges.

Microxaea. A minute oxea. Fig. 6b.

Monocrepsis. A uniaxial desma. Fig. 1k.

Monactinal. Term applied to a uniaxial spicule in which growth proceeds in only one direction from the point of origin. Thus only one ray is formed, the point of origin remaining at the end of the spicule, which may or may not be swollen.

Orthodiaene. A reduced orthotriaene in which the cladome includes but two rays. Fig. 3d.

Orthomonaene. Similar to a promanaene but the clad is at right angles to the rhabdome. Fig. 2c.

Orthotriaene. A triaene in which the clads make about a right angle with the rhabdome. Fig. 3e.

Oxea. A uniaxial spicule gradually pointed at each end. Fig. 1b.

Oxyaster. Hexact with small centrum, the rays taper to points. Fig. 1g.

Oxyhexaster. Hexact, principal rays of which divide into straight or bent terminals which run out to a point. Fig. 2g.

Pentact. Spicule with five rays; a reduced hexact. Fig. 15g.

Plagiotriaene. Triane in which the clads are directed forward, making an angle of about 45° with the rhabdome produced. Fig. 2e.

Prodiaene. A monaxon with two clads directed forward, making an obtuse angle with the rhabdome. Fig. 1d.

Promonaene. A monaxon with a single clad which forms an obtuse angle with the rhabdome. Fig. 1c.

Protocladus. The undivided part of a cladus.

Prototriaene. Triane in which the clads are directed forward, making an angle of less than 45° with the rhabdome. Fig. 4e.

Rhabdome. Shaft of a triaene. Fig. 2e.

Rhabdus. A rod-like, uniaxial spicule; with like or unlike ends.

Rhaphide. A long hair-like spicule. Fig. 5b.

Sagitta. Perpendicular distance from the origin of the cladome to the chord. (Line "S" in Figs. 1e and 4e.)

Sanidaster. Microsclere consisting of a rod-like axis, bearing spines along its whole length. Fig. 3g.

Sclere. Skeletal element or spicule.

Sigma. Microsclere shaped like the letter "C." Fig. 1m.

Sigmaspire. A rod-like microsclere spirally twisted. Fig. 2m.

Sphaerohexaster. Hexact, principal rays of which divide into terminals provided with spherical knobs at the ends. Figs. 4g.

Sphaeraster. Euaster in which centrum is large as compared with length of the rays. Figs. 5g and 6 g.

Spherule. A minute microsclere, more or less spherical in form. Fig. 10g.

Spiraster. Microsclere consisting of a spirally bent axis, bearing spines on its outer surface. Fig. 11g.

Spongin. The horny material uniting spicules, or (as in the Keratosa) constituting the skeleton.

Stauractine. A tetractine, the four rays of which form a cross.

Sterraster. Euaster with numerous rays which become soldered together. Fig. 7g.

Streplaster. A comprehensive term applied to asters in which the rays proceed from an axis, and not from a center.

Strongyle. A uniaxial spicule in which both ends are rounded, but not swollen. Fig. 3b.

Style or stylus. A uniaxial spicule with one end simply rounded off, the other pointed. Fig. 1a.

Tetracepis. A desma with four actines. Fig. 4k.

Tetractine. A hexact reduced to four actines. Fig. 1h.

Tetraxon. Spicule in which the rays develop along four axes.

Tornote. A uniaxial spicule in which both ends are abruptly pointed. Fig. 2b.

Toxa. A bow-shaped microsclere.

Triactine. A hexact reduced to three branches. Fig. 11e.

Triaene. A tetraxon in which a ray, distinguished as the shaft or rhabdome, bears at one end three other rays, the cladi.

Trichodragmata. Hair-like spicules in bundles. Fig. 3m.

Tricrepis. A desma with three actines. Fig. 3k.

Tylostylus. A uniaxial spicule pointed at one end, swollen at the other. Fig. 2a.

Tylote. A uniaxial spicule swollen at both ends. Used as an adjective with respect to any spicule ray, it implies that the ray is swollen or knobbed at the end. Fig. 4b.

Uniaxial. Term applied to a spicule in which growth proceeds along only one axis. Spicule (monaxon) is thus rod-like, though it may be straight, or somewhat curved, or even bent. Figs. 1a, 2a, 1b, 2b, 4b, 5b, and 6b.

General Description of Quadrant Spicules

The uniaxial type of spicule is represented by more specimens than any other form. They range in size from minute microxeas to individuals three-eighths of an inch long. They may be curved, straight, fusiform, or hairlike. Many of them are spotted with iron stains which are raised in round bumps. In some instances these spots represent the point of contact between two spicules. Types of monaxons which have been found in the Quadrant rocks include, oxeas, strongyles, styles, tylostyluses, tylotes, raphides, and trichodragmata. Oxeas are by far the most common of the group.

Asters are also abundant and well preserved. The euaster is the most common of this group and is second only to oxeas in abundance. Oxyasters

are the most common type of euaster. A few oxyhexasters are present, but the fauna is marked by an absence of both sphaerasters and chasters.

The third most important group of Quadrant spicules are representatives of the triaenes. Protriaenes and anatriaenes are about equal in number and range in length from 0.5 mm. to 5 mm.

Desmas are rather common. The tricrepis form is very distinctive, but is not as abundant as monocrepis.

Tetractines are not particularly abundant, but form some of the most beautiful and distinctive spicules within the fauna. Tetractines with spinose rays are especially diagnostic.

In spicule measurement, the aim has been to give an idea of the characteristic size, the extremes being excluded. For this reason the measurements given do not always coincide with the figured specimen. I have followed Wilson in adding *s* to form the plural of such words as clad, chela, toxa, etc. I have also followed him in using oxeate as the adjective in preference to oxeote.

Form Descriptions

AMPHIASTERS

Spicules with a long to short central bar with four or more actines radiating from each extremity.

Remarks.—In shape this form may be similar to an amphitriaene but is distinguished by the presence of more than three actines at each end. These spicules are not common in the Quadrant.

AMPHIASTER (a)

Plate 2, Fig. 1

Spicules with four short actines on each end of a shaft; actines rounded to blunt. Bar long, straight, cylindrical, uniform diameter. Length 1.6 mm.; length of actines 0.06 mm.; saggita 0.20 mm., diameter 0.12 mm.

Univ. of Illinois, x-1402.

PRODIAENES

Monaxial spicules with two forwardly directed cladi making an obtuse angle with the rhabdome.

PRODIAENE (a)

Plate 2, Fig. 3

Rhabdome broadly curved like the letter S, cylindrical, uniform diameter, one end bluntly terminated. The two cladi terminate acutely but expand rapidly forming a gibbous cladome; one clad forms an angle of about 125 degrees with the rhabdome and the other forms an angle of about 120 degrees, the angle between the cladi being 120 degrees. Without exact measurements the angles appear to be equal. Length 1.0 mm.; length of rhabdome 0.80 mm.; length of clad 0.20 mm.; chord 0.40 mm.; saggita 0.20 mm., diameter of rhabdome 0.08 mm.

Univ. of Illinois, x-1403.

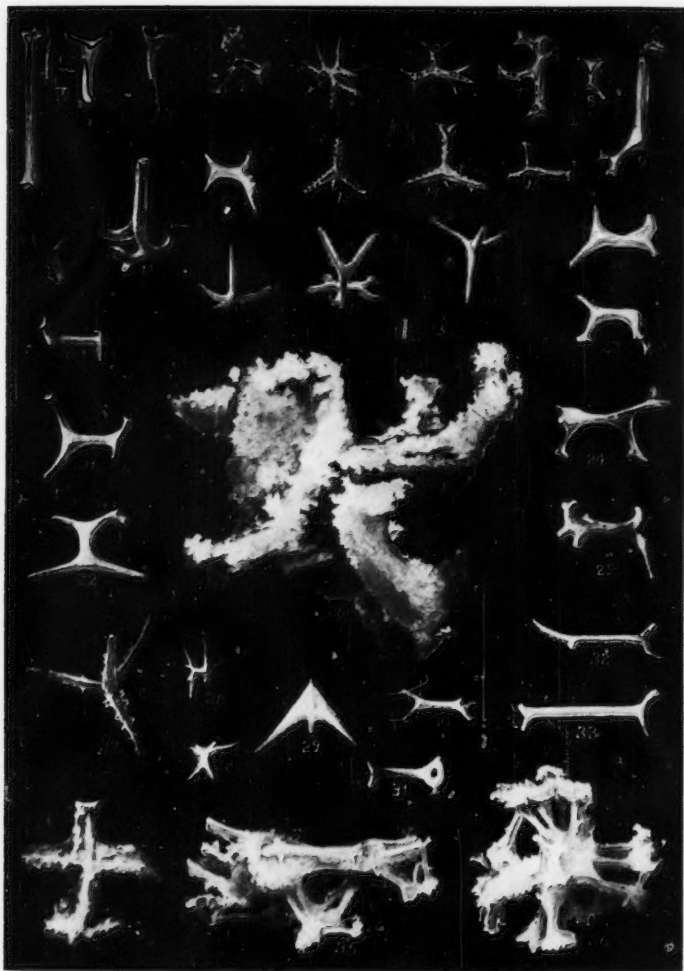


PLATE 2.—All figures on plates 2, 3, and 4 are from the Quadrant formation (Lower Pennsylvanian) at exposures on the south side of Jefferson Canyon near Cardwell, Montana. All figures approximately $\times 25$. Letters in parentheses refer to the form as described in the text. *Amphiasters*—1(a). *Amphidaenes*—2(b); 8(a); 10(d); 12, 20, 22(c); 21(f); 32, 33(e). *Prodiaene*—3(a). *Tricrepis*—4(a); 15(b). *Diarepis*—16(a). *Monocrepis*—7(a); 9(b); 11(c); 23(d); 24(e); 25(f); 30(g). *Trichotriaenes*

TRICREPIS

Desma-like spicules with three actines diverging from a common point.

Specimens belonging to this group are very abundant in the Quadrant samples.

TRICREPIS (a)

Plate 2, Fig. 4

Desma-like spicules with symmetrically arranged actines. Actines of equal length; two terminate in three short rounded clads, but the third actine, in addition to three small clads, is marked by two side protuberances, one of which is dichotomous. Outer angle between a clad and actine is about 140° . Actines, make an angle of 45° with a horizontal plane passed through the centrum. Centrum small. Length of actine 0.40 mm.; diameter of actine 0.10 mm.; chord 0.60 mm.

Univ. of Illinois, x-1404.

TRICREPIS (b)

Plate 2, Fig. 15

A desma with three actines of unequal length. Terminus of actines slightly enlarged into a flower-like (rosette) structure. Actines cylindrical, relatively long and delicate; angle between longest and shortest actine 160° , other two angles equal 100° each. Angle between actines and a horizontal plane passed through the centrum is about 25° . Length of actines: longest 0.40 mm., intermediate 0.30 mm., shortest 0.20 mm.; diameter of actines 0.06 mm.; chords: longest 0.70 mm, intermediate 0.55 mm, shortest 0.40 mm.

Univ. of Illinois, x-1405.

MONOCREPIS

Uniaxial desmas with two or more clads; the clads may or may not be divided into two or more distal divisions.

MONOCREPIS (a)

Plate 2, Fig. 7

Large desmas which bear four unsymmetrical clads near one end of the shaft; three of the clads are dichotomous, these distal divisions are short and rounded. Other end of shaft enlarges rapidly near terminus, forming an irregular knob-like structure. Greatest length, 1 mm.; length of longest clad 0.40 mm.; length of deuteroclads 0.08 mm.; width of shaft 0.12 mm.

Univ. of Illinois, x-1407.

MONOCREPIS (b)

Plate 2, Fig. 9

Desmas with a long, stout, nearly straight shaft bearing at one end a long actine which is divided into deuteroclads; the deuteroclads are dichotomously divided. At the same end, but on the opposite side of the shaft is a short

—5(a); 6(b). *Tetractines*—13(a); 14(b); 17(d); 18(c); 19(e); 27(f). *Orthodiaene*—29, cladome. *Phyllotriaene*—31, probably a broken specimen. *Stauractine*—34(a). Spicules of unknown affinities—26, 35, 36.

pointed actine. This may be a broken clad similar to its mate though the point cannot be determined. The other end of the shaft terminates in an enlarged triangular structure that is slightly concave in the central area; greatest concavity is at a point directly over the center of shaft. Length of shaft 1 mm.; diameter of shaft 0.16 mm.; length of actine 0.35 mm.; diameter of longest actine 0.08 mm.; length of deuteroclad 0.15 mm.

Univ. of Illinois, x-1408.

MONOCREPIS (c)

Plate 2, Fig. 11

Spicules with a stout shaft bearing actines on only one end. Cross-section of shaft circular. First actine simple, slightly curved, termination rounded; second actine dichotomous; deuteroclads recurved, almost as large as protocladus, one deuteroclad marked by a small side branch at about the mid-point. Length of shaft 0.70 mm.; diameter of shaft 0.14 mm.; length of simple actine 0.40 mm.; length of dichotomous actine 0.30 mm.; length of deuteroclads 0.40 mm.

Univ. of Illinois, x-1409.

MONOCREPIS (d)

Plate 2, Fig. 23

Desmas with two actines projecting from each end of the shaft. At one end of shaft the two actines form an angle of 30 degrees with each other; one actine is short and stout, forming angle of 90 degrees with the shaft; other actine is long and slender with a pronounced rosette on the termination. Actines at other end of shaft emerge on opposite sides, from an angle of 110 degrees with each other; one actine is terminated by a rosette and makes an angle of 105 degrees with shaft, other actine makes an angle of 130 degrees with shaft and termination is rounded. Greatest length 0.75 mm.

Univ. of Illinois, x-1410.

MONOCREPIS (e)

Plate 2, Fig. 24

Desmas with two long dichotomous actines at one end of shaft and the other end marked by a bulbous expansion from which one long and two short actines extend. Protoclads of dichotomous actines slightly twisted and two to three times as long as the deuteroclads; terminations of deuteroclads pointed to rounded; protocladus form angle of 90 degrees with each other.

Shaft smallest in central portion, expanding gradually toward the dichotomous actines and rapidly toward the bulbous end. Long actine extending from bulbous end terminated by rosette; two short actines are rounded to blunt (one may be broken). Greatest length 0.90 mm.; length of protocladus 0.25 mm., length of deuteroclads 0.05 to 0.15 mm.

Univ. of Illinois, x-1411.

MONOCREPIS (f)

Plate 2, Fig. 25

Desmas with three actines at one end of shaft, four near the other end. Two of the three actines at one end are stout, short and recurved; the third actine

is long and slender, and protrudes from the opposite side of shaft. Four actines at other end of shaft are short, stout, and bluntly terminated; two are side branches protruding from opposite sides at right angles to the shaft 1 mm. from its end; the other two, one of which is dichotomous, protrude from near end of shaft. Greatest length 0.60 mm.

Univ. of Illinois, x-1412.

MONOCREPIS (g)

Plate 2, Fig. 30

Desmas with a straight slender shaft bearing two actines at one end and three on the other. Two actines at one end emerge at angle of 120 to 150 degrees, rounded terminations, about half as long as shaft. Actines at opposite end of shaft short, do not emerge from same point, terminations rounded. Length of shaft 0.40 mm.; diameter of shaft 0.08 mm.; length of longest actines 0.20 mm.

Univ. of Illinois, x-1413.

TETRACTINES

Four-rayed spicules; actines may or may not bear small spines; one or more of the rays may bifurcate.

Remarks.—This form is not to be confused with *Rhakistella* J. M. Weller. *Rhakistella* is characterized by the presence of six rays and is an aster.

TETRACTINE (a)

Plate 2, Fig. 13

Symmetrical spinose tetractines; rays of equal length and similar shape, uniformly grade in size from acute terminations to centrum; actines form angles of about 125 degrees with each other, covered with small equally sized and spaced spines, 5 to 6 spines in a row from centrum to termination of actine. Actines are so arranged that any ray passing through an apex of a tetrahedron makes equal angles with the three edges which form the apex. Length of actines 0.40 mm.; width of actines 0.05 mm.

Univ. of Illinois, x-1415.

TETRACTINE (b)

Plate 2, Fig. 14

Spinose tetractines with three lateral rays of equal length and similar shape and a longer vertical ray. Vertical ray dichotomous; deuteroclads short, forming an angle of 90 degrees with one another. Vertical actine forms an angle of about 100 degrees with lateral rays. All actines covered with small equally sized and spaced spines, about 5 spines in a row from centrum to terminations. Centrum slightly above a plane which passes through terminations of lateral actines. Length of lateral actines 0.50 mm.; length of vertical actine 0.52 mm.; length of deuteroclads 0.12 mm.; maximum diameter of actines 0.14 mm.

Univ. of Illinois, x-1416.

TETRACTINE (c)

Plate 2, Fig. 18

Spinose tetractines, each ray of which is dichotomous. The three lateral

rays are in the same horizontal plane; they form a 120 degree angle with each other, and a 90 degree angle with the vertical ray. Protoclads and deuteroclads of lateral rays equal in length, terminations rounded; deuteroclads form an angle of 60-70 degrees with each other. Deuteroclads of vertical ray longer than protoclad, forming an angle of 70 degrees with each other, terminations rounded to pointed. Centrum in a plane containing lateral rays. All protoclads and deuteroclads sparsely set with minute spines. Length of lateral ray protoclads 0.16 mm.; length of lateral ray deuteroclads 0.20 mm.; length of vertical ray protoclad 0.25 mm.; length of vertical ray deuteroclads 0.50 mm.

Univ of Illinois, x-1417.

TETRACTINE (d)

Plate 2, Fig. 17

Spinose tetractines whose three lateral rays are slightly recurved so that their concave surface is on the side of the vertical ray. Vertical ray slightly the largest and longest; all rays thicken uniformly from acute terminations to centrum. Lateral rays form angles of 120 degrees with each other and an angle of about 90 degrees with vertical ray. Terminations of lateral rays lie in same plane; centrum below said plane. All rays sparsely set with minute spines. Length of vertical rays 0.50 mm.; length of lateral rays 0.35 mm.

Univ. of Illinois, x-1418.

TETRACTINE (e)

Plate 2, Fig. 19

Spinose tetractines, whose vertical ray is shorter than the lateral rays. Lateral rays form angles of 120 degrees with each other and 90 degrees with the vertical ray. Terminations rounded to pointed; they tend to be slightly curved downward, and thicken uniformly from terminations to centrum. Rays covered by numerous minute spines. Centrum slightly above plane containing terminations of lateral rays. Length of vertical ray 0.30 mm.; length of lateral rays 0.50 to 0.60 mm.

Univ. of Illinois, x1-419.

TETRACTINE (f)

Plate 2, Fig. 27

Tetractines whose rays are set with relatively large spines or nodes that are about as thick as long. Lateral rays form angles of 120 degrees with each other and 90 degrees with the vertical ray. Lateral rays broadly arched so that convex surface is on the side of the vertical ray. Rays of equal length, uniformly thickening from acute terminations to centrum. Horizontal plane containing terminations of lateral rays lies slightly below centrum. Length of rays 0.90 mm.

Univ. of Illinois, x-1420.

TRICHOTRIAENES

Symmetrical spicules with three rays emerging from a common center, each ray trichotomous; actines spinose or free of spines.

TRICHOTRIAENE (a)

Plate 2, Fig. 5

Spicules with three short rays emerging from the centrum. Each ray trichotomous; distal divisions of equal length and shape, enlarging uniformly from acute terminations to point of division, and set with small equally spaced and sized spines. Distal divisions form 90 degree angle with each other and about 110 degrees angle with primary rays. Primary rays form angle of 120 degrees with each other. Centrum not enlarged. Length of distal divisions 0.30 mm.; length of primary rays 0.16 mm.

Univ. of Illinois, x-1421.

TRICHOTRIAENE (b)

Plate 2, Fig. 6

Spicules with three stout trichotomous rays emerging from centrum. One ray forms angles of about 110 to 118 degrees with the other two. Distal divisions straight to slightly curved; terminations sharply pointed to rounded; angles formed with each other and primary rays not consistent. Centrum not enlarged. Length of distal divisions 0.16 mm.; length of primary rays 0.20 mm.; diameter of primary rays 0.08 mm.

Univ. of Illinois, x-1422.

AMPHIDAENES

Simple spicules consisting of a shaft with two clads on each end.

Remarks.—It is often difficult to distinguish between amphidaenes and certain monocreps types. In general monocreps is more gnarled and irregular.

AMPHIDAENES (a)

Plate 2, Fig. 8

Nearly symmetrical spicules with two actines on each end of the shaft. Shaft short, sides broadly curved from points of actines. Cross-section of shaft slightly elliptical. Actines well developed, one-half as long as shaft, terminations rounded to pointed. Actines form angles of about 120 degrees with shaft. Chord 0.25 mm.; length 0.35 mm.; diameter of shaft 0.08 mm.

Univ. of Illinois, x-1423.

AMPHIDIAENE (b)

Plate 2, Fig. 2

Desmas with two actines at each end of the shaft; paired actines at each end of shaft lie in planes at right angles to each other. Shaft straight to slightly curved, circular in cross-section. Actines at one end of shaft very short; other pair of actines about one-half to one-third as long as shaft, terminations rounded, diameter equal to that of the shaft. Actines form angles of 120 degrees. Length of shaft 0.60 mm.; diameter of shaft 0.12 mm.; length of longer actines 0.32 mm.; diameter of longer actines 0.12 mm.

Univ. of Illinois, x-1424.

AMPHIDIAENE (c)

Plate 2, Fig. 12, 20, 22

Spicules consisting of a shaft with two actines at each end. The four actines lie in a plane containing the shaft and emerge at an angle of about 105 degrees; angle between actines 150 degrees. Two actines at one end of shaft are of equal length and uniformly increase in size from acute terminations to shaft. Other two actines are of unequal length and dissimilar in shape; one simple and unmodified, the other marked by one or two nodes. Sides of shaft and actines form broad U-shaped curve.

Univ. of Illinois, x-1425.

AMPHIDIAENE (d)

Plate 2, Fig. 10

Desmas with a short shaft bearing two actines at each end. Actines longer than shaft, straight to curved, pointed to rounded at terminations; one actine considerably larger than other three. Sides of shaft and actines form U-shaped curve; actines emerge at angle of 120 degrees. One of the actines is dichotomous near termination.

Remarks.—This type is distinguished from types (a) and (c) by the short shaft and unequal actines.

Univ. of Illinois, x-1426.

AMPHIDIAENE (e)

Plate 2, Figs. 32, 33

Desmas with a long, straight shaft bearing two actines at each end; shaft of uniform thickness, its sides parallel. Actines at one end of shaft emerge at angles of 100 to 120 degrees, forming broad smooth curve with one another; terminations rounded. Actines at opposite end of shaft are circular in cross-section; terminations rounded. Length of shaft 1.1 mm.; diameter of shaft 0.10 mm.

Univ. of Illinois, x-1427.

AMPHIDIAENE (f)

Plate 2, Fig. 21

Desmas with two dissimilar actines at each end of a shaft. Actines at one end of shaft short, straight; termination of one acute, of other flower-like. Actine with acute termination emerges from shaft at angle of 80 degrees, the other at angle of 100 degrees. Actines at opposite end of shaft long, slightly curved; terminations of one acute, of other flower-like; actines emerge from shaft at angle of 120 degrees. Actines with similar terminations on same side of shaft. Length of shaft, 0.45 mm.; diameter of shaft, 0.08 mm.; length of long actines, 0.45 mm.; length of short actines, 0.20 mm.

Univ. of Illinois, x-1428.

DICREFIS

Desmas with two actines emerging from a common point.

DICREPIS (a)

Plate 2, Fig. 16

Spicules with two actines emerging from a common center; one ray one-half to one-third as long as second. Long ray straight, uniform in thickness, with flower-like termination. Short ray thicker than long ray, terminating in two small points, and forming an angle of 90 to 100 degrees with long ray. Length of long ray 0.50 mm.; diameter of long ray 0.10 mm.; length of short ray 0.20 mm.; diameter of short ray 0.10 mm.

Univ. of Illinois, x-1429.

STAURACTINE

Tetractines in which the four rays form a cross.

Remarks.—The form described below is provisionally referred to this group. I have been unable to find a group name which has been applied to stauractine spicules, the actines of which are connected by inter-ray flanges.

STAURACTINE? (a)

Plate 2, Fig. 34

Four rayed spicules arranged in the shape of a cross. Rays straight to slightly curved, terminations irregular, lateral flanges moderately developed in each quadrant. Surface rough. Length of rays 0.60 to 0.80 mm.; thickness of rays 0.20 mm.

Univ. of Illinois, x-1430.

STAURACTINE (b)

Plate 3, Fig. 34

Four-rayed spicules. Actines long, slender, uniform in thickness, with acute terminations. Centrum small. Greatest length of actines 0.50 mm.; diameter of actines 0.04 mm.

Univ. of Illinois, x-1431.

OXEAS

Uniaxial spicules, straight or curved, pointed at both ends.

Remarks.—The name *Petrosites* was proposed by Howell and Landes (Jour. Paleo. v. 10, no. 1, p. 58, 1936) as a form genus to include oxeate sponge spicules. The genus was described as:

A form genus to include simple, diactinal spicules of the following description. Spicule oxeote, cylindrical, smooth, without nodes; straight or gently curved. Curvatures generally symmetrical, without defined locus of curvature. Spicule of fairly uniform diameter or tapering faintly to points near the end, where rapid tapering begins. Terminations acute or slightly rounded, formed by a break in the concave curve when the spicule is viewed in a position showing curvature. Axial canal terminates within the spicule.

Oxeas are among the most abundantly represented types of sponge spicules, both fossil and modern. Fossil spicules belonging to this group have also been classified as *Reniera*, but *Reniera* Nards 1847 is the generic name of a modern sponge and cannot properly be retained for isolated fossil spicules. *Petrosites*, when used, must be considered as a form genus including oxeas. However, not all fossil oxeas are related to the modern genus *Petrosia*, for oxeas common

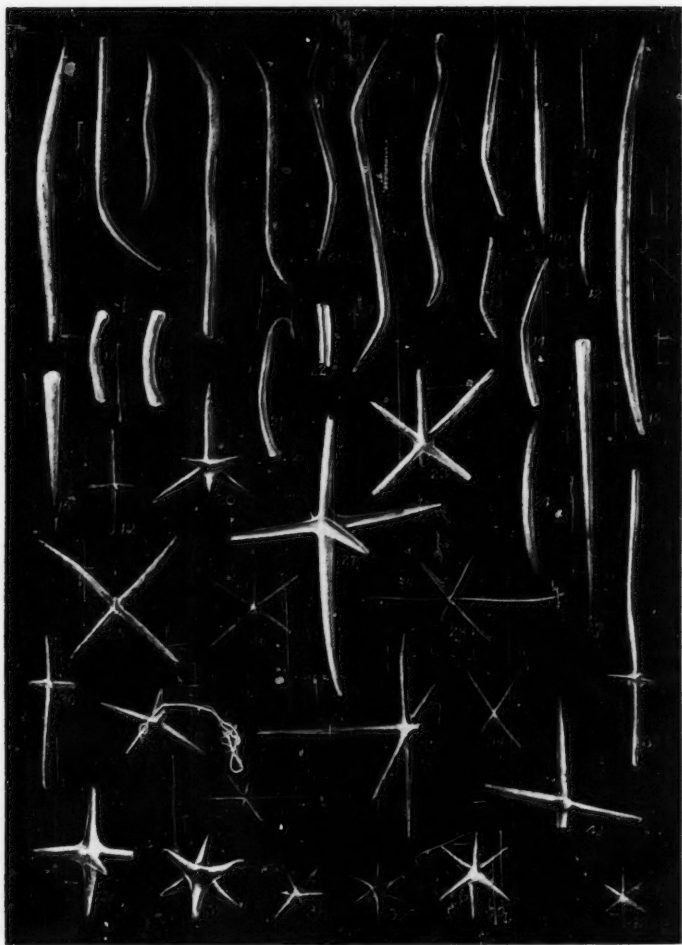


PLATE 3.—*Oxeas*—1(c); 3(d); 5-7(e); 10(a); 11(f); 12, 15, 24(b). *Promonacnes*—2, 4(a); 9, 13(b). *Styles*—8(c); 14(b); 29(a). *Tylostyle*—16(a). *Tyloles*—17, 18(a). *Oxyasters*—19, 28, 30, 32(b), 20(c); 23, 27, 33(d); 25, 41(e); 26(f); 35(g); 37(h); 38(i); 39, 40, 42(a). *Trichodragmata*—22(a). *Pentacts*—31, 36(a). *Stauractine*—34(b).

ly occur in such modern genera as *Erylus*, *Characella*, *Poecillastra*, *Geodia*, *Jaspis*, *Tetilla*, *Strongylophora*, *Paratetilla*, *Petrosia*, *Phloeodictyon*, *Gellius*, *Myxilla*, *Costifer* and other genera which belong to several families and sub-orders of Tetraxonida. Use of the name *Petrosites* Howell and Landes would indicate that *Petrosia* had its beginning in Ordovician times.

Fossil oxeate spicules are generally placed in the order Monactinellida, but continuance of that procedure can only lead to confusion and misconceptions. At present I prefer to describe them under the biological form name.

OXEA (a)

Plate 3, Fig. 10

Straight oxeas; thickest near the center, tapering gradually to sharp points on both ends, circular in cross-section. Length 2 mm.; greatest width 0.12 mm. *Univ. of Illinois*, x-1432.

OXEA (b)

Plate 3, Figs. 12, 15, and 24

This type of sponge spicule was described by J. M. Weller as *Reniera siliqua* (*Jour. Paleo.* 4:236, Pl. 15, figs. 6-12, 1930).

Weller's description:

The detached spicules of this species are cylindrical, smooth and curved. The specimens observed average about 2mm. in length and are all rather uniformly about 0.2 mm. in thickness. The spicules commonly taper slightly toward both extremities and may terminate in round blunt ends or project more acutely. The curvature is gentle and more or less uniform. The more curved forms present a slight suggestion of angularity. In the least curved specimens the inside edge of the spicule is nearly straight and the curve of the outer edge is determined by the tapering of the spicule toward the ends.

Remarks.—I would not include in this type those forms possessing round or blunt ends.

Occurrence.—Lower Pennsylvanian, Rock Island County, Illinois; Quadrant, Jefferson Canyon, Cardwell, Montana.

Measurements.—Length 0.75 mm. to 4.50 mm.; thickness 0.05 mm. to 0.20 mm.

Univ. of Illinois, x-1433.

OXEA (c)

Plate 3, Fig. 1

Relative large oxeas. Greatest thickness near point of greatest curvature; loci of curvature nearer one end, ratio of parts averaging 2:3. Terminations tend to be recurved toward the convex side of the spicule. Length 2.50 mm.; greatest diameter 0.25 mm.

Univ. of Illinois, x-1434.

OXEA (d)

Plate 3, Fig. 3

Oxeas marked by a pronounced concavity at the midpoint of the spicule on the convex side. Greatest diameter at center, tapering gradually to acute terminations. Length 2 mm.; greatest diameter 0.12 mm.

OXEA (e)

Plate 3, Figs. 5, 6, and 7

Relative large oxeas marked by fairly sharp curvatures near each termination. Terminals curved in opposite direction so that lines drawn from each end of spicule through the nearest point of curvature are parallel; loci of curvatures located so that the ratio of the parts is 1:3:1. The sides of the central and longer division are parallel; from points of curvature the spicule grades gradually to acute terminations. Length 2 mm. to 3 mm.; length of central portion 1 mm. to 2 mm.; greatest width 0.12 mm.; distance from loci of curvature termination 0.50 mm. to 0.75 mm.

Univ. of Illinois, x-1436.

OXEA (f)

Plate 3, Fig. 11

Straight, hairlike oxeas; diameter fairly uniform throughout length. Terminations acute. Average length 1.20 mm.; diameter 0.02 mm. to 0.04 mm.

Remarks.—Weller pictures similar forms from the Lower Pennsylvanian of Illinois.

Univ. of Illinois, x-1437.

PROMONAENES

Simple monaxons with a single clad which forms an obtuse angle with the rhabdome.

PROMONAENE (a)

Plate 3, Figs. 2, 4

Large to medium sized; loci of curvature near one end, ratio of parts ranging from 1:4 to 1:6. Sides of rhabdome parallel; clad tapers gradually to a slightly rounded point and joins rhabdome in a smooth curve. Clad 0.80 mm.; rhabdome 2 mm.

Univ. of Illinois, x-1438.

PROMONAENE (b)

Plate 3, Figs. 9, 13

Small to medium-sized promonaenes; ends of clad and rhabdome rounded. Proportions similar to those of type (a); distinguished from that form by the rounded end of the clad, and the fact that the clad forms a larger angle with the rhabdome. Clad 0.40 mm.; rhabdome 1.40 mm.

Remarks.—These forms might be confused with strongyles. They are distinguished from that group by the presence of a clad. If the bend is fairly sharp and near one end it is considered as a clad. Broken oxeas (e) and (f) are very similar in shape to promonaenes.

Univ. of Illinois, x-1439.

STYLES

Simple uniaxial spicules with one end rounded off, the other pointed.

STYLE (a)

Plate 3, Fig. 29

Spicules gradually tapering from an acute termination at one end to a blunt termination at the other. Spicule straight, smooth, symmetrical. Greatest diameter at blunt end. Length 3 mm.; greatest diameter 0.20 mm.; diameter at mid-point 0.10 mm.

Univ. of Illinois, x-1440.

STYLE (b)

Plate 3, Fig. 14

Broadly curved styles. Thickness uniform from rounded end to locus of curvature, where remainder of spicule gradually tapers to acute point; loci of curvature centrally situated. Length 1.60 mm.; diameter 0.08 mm.

Univ. of Illinois, x-1441.

STYLE ? (c)

Plate 3, Fig. 8

Spicules smooth, cylindrical; one termination acute, the other blunt. Terminations curve toward convex side of broadly curved central portion; ratio of parts about 1:6:1. Blunt termination slightly recurved. Gradual thickening from acute termination to locus of nearest curvature, uniform thickness throughout the remainder of spicule. Length 3 mm.; diameter 0.10 mm.

Univ. of Illinois, x-1442.

TYLOSTYLES

Straight to curved uniaxial spicules pointed at one end, swollen or knobbed at the other.

TYLOSTYLE (a)

Plate 3, Fig. 16

Straight spicules uniformly enlarging from an acute termination to a point near the other end where it changes abruptly to a small swollen knob. Length 1.50 mm.; maximum diameter 0.04 mm.

TYLOTES

Straight to curved uniaxial spicules, swollen or knobbed at both ends.

TYLOTE (a)

Plate 3, Figs. 17, 18

Spicules relatively short, stout, cylindrical, broadly curved and knobbed at both ends. Uniform in thickness from knob to knob. Curved along entire length; loci of curvature central to slightly sub-central. Ends of knobs rounded. Length 1 mm.; diameter 0.14 mm.; diameter of knob 0.17 mm.

Univ. of Illinois, x-1444.

TRICHODRAGMATA

Slender oxate spicules that occur in bundles.

TRICHODRAGMATA (a)

Plate 3, Fig. 22

Spicule bundle consists of two individuals of equal sizes. Both are slender, smooth, and cylindrical; straight to very slightly curved. Terminations blunt. Diameter fairly uniform throughout length. Length 0.60 mm. to 2 mm.; diameter of one individual 0.08 mm.

Univ. of Illinois, x-1445.

PENTACT

Five-rayed spicules, representing hexacts with one reduced ray.

PENTACT (a)

Plate 3, Figs. 31, 36

Five-rayed asters; four actines of similar shape and size, slightly flattened on under side, lie in same plane; cross-section of fifth (or vertical) actine is circular, slightly shorter than lateral rays, under side of lateral rays slightly flattened to broadly convex. Actines acutely terminated, uniformly enlarging to centrum. Centrum moderately thick; edge of centrum between actines rounded. Length of actine 0.60 mm.; maximum diameter of actine 0.30 mm.; diameter of centrum 0.30 mm.

Remarks.—This type is a common form in the Quadrant collections from Jefferson Canyon. Some specimens are transparent but others are milky white and opaque.

Univ. of Illinois, x-1446.

OXYASTERS

Euasters in which six actines proceed from a common center; actines, or rays, taper to a point (never knobbed); centrum small.

Remarks.—For convenience in description all asters are so oriented that the longest rays are vertical and are designated the *a* axis; rays of intermediate length, the *b* axis; and the shortest rays, the *c* axis. Specimens should be figured with the *a* axis vertical, but the figures in this report were drawn before the importance of that point was realized, and consequently, a few specimens are poorly oriented. In giving the axial ratio the *b* axis is considered as one; therefore, except in cases where the axial ratio is 1:1:1, *a* will be greater than one and *c* will usually be less than one.

OXYASTER (a)

Plate 3, Figs. 39, 40, 42

Symmetrical asters with straight, equally long, similarly shaped and sharply pointed actines. Centrum small to slightly enlarged; actines uniformly enlarge from acute terminations to centrum. Axial ratio; 1:1:1.

Univ. of Illinois, x-1447.

OXYASTER (b)

Plate 3, Figs. 19, 28, 30, 32

Euasters with straight to slightly curved actines. Centrum not enlarged;

actines slender, of uniform thickness to a point near the end, where they taper rapidly to a sharp point. Axial ratio; 2:1:0.5.

Univ. of Illinois, x-1448.

OXYASTER (c)

Plate 3, Fig. 20

Euasters with one actine of each axis reduced. Long actine of *a* axis stout, uniform thickness from centrum to point near termination where it rapidly tapers to a sharp point; reduced actine one-third to one-fourth length of longer one, tapers from acute termination to centrum, *b* and *c* axes equal in length; actines uniformly enlarge from pointed terminations to centrum, short actines about one-half length of longer ones. Centrum moderately developed. Axial ratio: 1.1:1:1.

Univ. of Illinois, x-1449.

OXYASTER (d)

Plate 3, Fig. 23, 27, 33

Large asters with straight to slightly curved long actines. Centrum small, actines uniformly enlarge from acute terminations to centrum; actines of *a* axis may be slightly curved, those of *b* and *c* axes straight. Axial ratio: 1.2:1:0.6.

Univ. of Illinois, x-1450.

OXYASTER (e)

Plate 3, Figs. 25, 41

Eusters with straight to slightly curved actines; actines of *c* axis greatly reduced. Actines increase uniformly in size from sharp terminations to centrum; centrum not enlarged. Ratio of axes: 1:1:0.12.

Measurements.—*A* axis 1 mm.; *B* axis 1 mm.; *C* axis 0.12 mm.

Univ. of Illinois, x-1451.

OXYASTER (f)

Plate 3, Fig. 26

Euasters with straight, long, and slender actines which meet in an enlarged centrum. Actines terminate in sharp points. Similar to type *b* but differs from that form by the presence of a bulbous centrum. Axial ratio: 1.2:1:0.75.

Univ. of Illinois, x-1452.

OXYASTER (g)

Plate 3, Fig. 35

Euasters with the *a* axis greatly elongated. Individual actines of uniform thickness, those of *b* and *c* axes very short and smaller in circumference than those of *a* axis; terminations probably acute. Centrum not enlarged. Axial ratio (approximate); 7:1:1.

Univ. of Illinois, x-1453.

OXYASTER (h)

Plate 3, Fig. 37

Small asters with thick centrum and fairly short stout actines. Axial ratio: 1:1:1.

Remarks.—Type *h* is similar to type *a* but differs from it by the rapidly enlarging actines.

Univ. of Illinois, x-1406.

OXYASTER (i)

Plate 3, Fig. 38

Small asters with straight sharply pointed actines; actines uniformly enlarge from terminations to centrum. Centrum slightly enlarged. Axial ratio; 1.8:1:0.9 to 2:1:1.

Remarks.—This type is similar to type *a*. It differs only in the greater length of the *a* axis. Length, *a* axis 0.40 mm.; *b* axis 0.25 mm.; *c* axis 0.25 mm.

Univ. of Illinois, x-1454.

ANATRIAENES

Triaene spicules in which the shaft bears at one end three posteriorly directed clads.

ANATRIAENE (a)

Plate 4, Fig. 1

Spicules consisting of a long shaft bearing three posteriorly directed clads at one end. Shaft long, cylindrical, uniform in thickness, not tapered. Clads long, uniformly and gently curved; they enlarge from sharply pointed terminations to cladome and form angles of 120 degrees with each other and an angle of 50 to 60 degrees with the shaft. Apex of cladome sharply rounded. Chord 0.16 mm.; sagitta 0.40 mm.; shaft 1 mm.; width of shaft 0.06 mm.; length of clads 0.34 mm.

Remarks.—This type differs from the spicules described as *Geodites? deflecturus* by J. M. Weller in the sharply rounded cladome and length and curvature of clads.

Univ. of Illinois, x-1455.

ANATRIAENE (b)

Plate 4, Fig. 14

Geodites? deflecturus J. M. Weller, 1930, Jour. Paleo. 4(3):240, pl. 16, figure 32, 33.

Spicules consisting of a long rhabdome with three posteriorly directed clads at one end. Rhabdome cylindrical, uniform in thickness, does not taper. Clads joined to shaft at right angles, uniformly and gently curved to sharp terminations, form angles of 120 degrees with each other. Apex of cladome slightly curved to flat. Chord 0.25 mm.; sagitta 0.12 mm.; length of clads 0.20 mm.; length of shaft 0.50 mm.

Univ. of Illinois, x-1456.

ANATRIAENE (c)

Plate 4, Figs. 10, 19

Spicules consisting of a rhabdome bearing three slender, broadly curved clads at one end. Apex of cladome sharply rounded. Chord 0.30 mm.; sagitta 0.30 mm.; length of clads 0.18 mm.; length of shaft 0.50 mm.

Univ. of Illinois, x-1414.

ANATRIAENE (d)

Plate 4, Fig. 7

Spicules consisting of a rhabdome which bears three recurved clads at one end. Rhabdome uniformly enlarges from termination to cladome. Clads moderately long, sharply pointed, gently and uniformly curved; they form angles of 30 degrees with shaft and 120 degrees with each other. Shaft merges laterally and upward with clads, forming a broadly concave surface between clads; upper half of clads fused into a thick cladome pointed at the apex. Chord 0.18 mm.; sagitta 0.18 mm.; length of clads 0.12 mm.; length of shaft 0.50 mm.

Univ. of Illinois, x-1457.

PLAGIOTRIAENES

Triaenes in which the clads are directed forward, making an angle of about 45 degrees with the rhabdome produced.

Remarks.—Plagiotriaenes have been included by some workers under the genus *Geodites* Carter. Plagiotriaenes occur in many modern genera and are often associated with many different kinds of spicules. In *Geodia sparsa* Wilson occur oxeas, styles, anatriaenes, protriaenes, sterrasters, and plagiotriaenes. To attempt to classify spicules under such names as *Geodites* can only result in nomenclatural chaos.

PLAGIOTRIAENE (a)

Plate 4, Fig. 8

Plagiotriaenes with a very long rhabdome and three short forwardly directed clads. Shaft gradually increases in thickness from termination to a point about four-fifths of the distance to the cladome, where the maximum inflation is reached: remaining portion of shaft rapidly decreases in thickness to base of cladome. Clads straight, short, sharply pointed, forming an angle of 45 degrees with shaft. Cladome narrow. Chord 0.16 mm.; sagitta 0.08 mm.; length of clads 0.10 mm.; length of shaft 2 mm.; maximum diameter of shaft 0.12 mm.; diameter of shaft below cladome 0.06 mm.

Univ. of Illinois, x-1458.

PLAGIOTRIAENE (b)

Plate 4, Fig. 16

Rhabdome uniformly increases in diameter from termination to cladome. Clads straight, increasing uniformly in diameter from slightly rounded terminations to cladome and forming angles of 55 degrees with shaft. Cladome broad. Chord 0.36 mm.; sagitta 0.10 mm.; length of clads 0.20 mm.; length of shaft 0.60 mm.; diameter of shaft 0.04 mm.

Univ. of Illinois, x-1461.

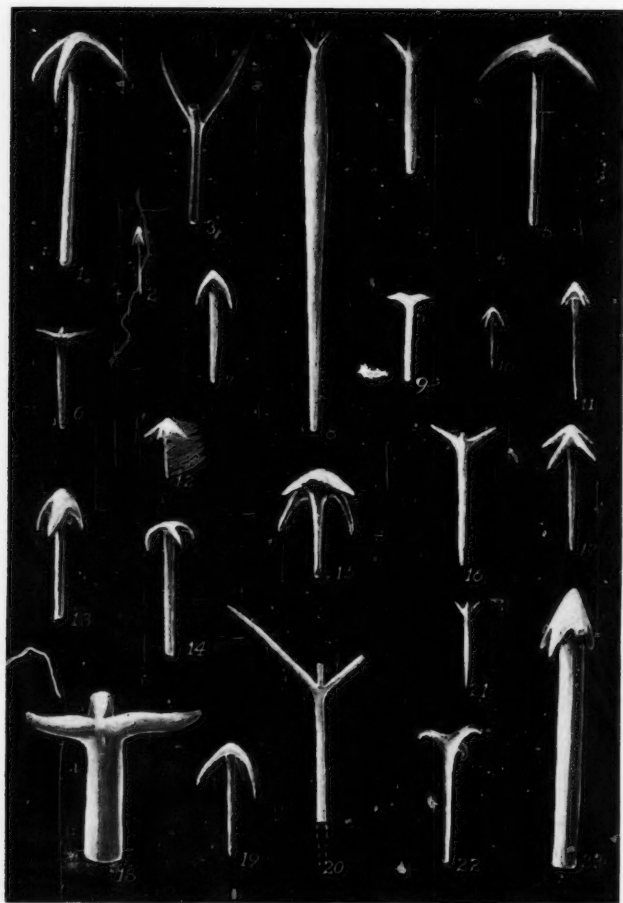


PLATE 4.—*Anatriaenes*—1(a); 7(d); 10, 19(c); 14(b). *Analetraenes*—2(e); 5(d); 11(f); 12, 17(b); 13(a); 15(g); 23(c). *Plagiotriaenes*—3, 20(e); 4, 21(d); 8(a); 16(b); 22(c). *Orthotriaenes*—6(a); 18(b). *Orthodiaene*—9(a).

PLAGIOTRIAENE (c)

Plate 4, Fig. 22

Rhabdome tapers slightly from terminus to cladome. Clads emerge from shaft at angle of 45 degrees; broadly curved for two-thirds of their length; outer one-third sharply curved downward; terminations rounded. Cladome broad. Chords 0.36 mm.; sagitta approaches zero; length of clads 0.20 mm.; length of shaft 0.60 mm.; diameter of shaft 0.05 mm.

Univ. of Illinois, x-1462.

PLAGIOTRIAENE (d)

Plate 4, Figs. 4, 21

Rhabdome increases in thickness from acute termination to a point midway to cladome where maximum inflation is reached; slightly decreases in diameter to base of cladome. Clads straight and short, with acute terminations; they make angles of 45 degrees with shaft. Cladome broad. Chord 0.20 mm.; sagitta 0.10 mm.; length of clads 0.12 mm.; length of shaft 0.60 mm.; maximum diameter of shaft 0.08 mm.

Univ. of Illinois, x-1463.

PLAGIOTRIAENE (e)

Plate 4, Fig. 3, 20

Hysitrispongia carbonaria Ulrich, 1890, Illinois Geol. Surv. 8:245, pl. 6, figure 3.

Geodites carbonarius (Ulrich) J. M. Weller, 1930, Jour. Paleo., 4(3):239, pl. 15, figures 24-26 (not figures 33-36).

Rhabdome long, uniform in thickness. Clads long and slender, with acute terminations; they form angles of 45 degrees with shaft. Cladome narrow. Chord 0.50 mm.; sagitta 0.40 mm.; length of clads 0.60 mm.; maximum diameter of clads 0.04 mm.; diameter of shaft 0.06 mm.; length of shaft 1 mm.

Univ. of Illinois, x-1464.

ORTHOTRIAENES

Triaenes in which the clads make approximately a right angle with the rhabdome.

ORTHOTRIAENE (a)

Plate 4, Fig. 6

Rhabdome uniformly increases in diameter from blunt termination to cladome. Clads straight, increase uniformly in diameter from acute termination to cladome, and form angle of 90-95 degrees with shaft. Cladome thick. Chord 0.30 mm.; sagitta 0.06 mm.; length of clads 0.16 mm.; length of shaft 0.50 mm.

Univ. of Illinois, x-1459.

ORTHOTRIAENE (b)

Plate 4, Fig. 18

Rhabdome very thick; length unknown. Clads emerge from shaft at angle approaching 90 degrees; terminations acute to slightly rounded. Clads stout,

outer one-third slightly upturned forming concave-convex margin. Chord 1.5 mm.; sagitta approaches zero; length of clads 0.50 mm.; length of shaft 0.60 mm.; diameter of shaft 0.20 mm.; greatest diameter of clads 0.12 mm.

Univ. of Illinois, x-1460.

ANATETRAENES

Spicules consisting of a shaft which bears four posteriorly directed clads at one end.

ANATETRAENE (a)

Plate 4, Figs. 13

Rhabdome straight, uniform in thickness. Clads rapidly expand from acute terminations into broad cladome, and fuse laterally at mid-point; edges of any two clads form broad U-shaped curve. Surface from clad termination to apex of cladome uniformly and broadly rounded; apex of cladome rounded. Clads form angles of 45 degrees with shaft.

Univ. of Illinois, x-1465.

ANATETRAENE (b)

Plate 4, Figs. 12, 17

Rhabdome uniformly enlarges from termination to cladome. Clads mostly discrete; they increase slightly in size to point of fusion with cladome; surface from clad termination to apex of cladome straight and forms angles of about 50 degrees with shaft. Cladome broad, apex rounded. Chord 0.20 mm.; sagitta 0.14 mm.; length of clads 0.12 mm.; length of shaft 0.50 mm.; maximum diameter of shaft 0.05 mm.

Univ. of Illinois, x-1466.

ANATETRAENE (c)

Plate 4, Fig. 23

Rhabdome long, very thick, smooth, cylindrical. Clads short, forming angles of 20 to 30 degrees with shaft; elliptical in cross-section. Surface from clad termination to apex of cladome straight. Clads discrete for slightly less than one-half the distance to the cladome apex, but merge into large smooth cone-shaped cladome. Chord 0.14 mm.; sagitta 0.34 mm.; length of discrete clad 0.14 mm.; diameter of shaft 0.14 mm.; length of shaft 1.4 mm.

Univ. of Illinois, x-1467.

ANATETRAENE (d)

Plate 4, Fig. 5

Rhabdome apparently of uniform thickness. Two clads lying in one plane uniformly increase in size from acute terminations to cladome; they curve smoothly from point to point, their curvature forming a large arc of a circle. The other two clads which lie in a plane normal to the first are greatly reduced, forming sharp nodes. Chord 0.50 mm.; sagitta 0.20 mm.; length of discrete portion of clads 0.30 mm.; length of discrete portion of clads 0.30 mm.; length of shaft 0.80 mm.; diameter of shaft 0.07 mm.

Univ. of Illinois, x-1468.

ANATETRAENE (e)

Plate 4, Fig. 2

Rhabdome tapers slightly from termination to cladome. Outer sixth of clads discrete; remaining portion fused into well-developed cladome, its apex flat to slightly rounded. Clads form angles of 25 degrees with shaft; they form narrow ridges which cannot be traced to apex of cladome but fuse into smooth cone. Fused portion between clad ridges forms depressed-triangular area. Surface from apex of cladome to clad termination straight. Chord 0.06 mm.; sagitta 0.03 mm.; length of shaft 0.14 mm.; diameter of shaft 0.02 mm.

Univ of Illinois, x-1469.

ANATETRAENE (f)

Plate 4, Fig. 11

Rhabdome uniformly tapers from pointed terminations to cladome. Upper five-sixths of clads fused into broad cladome. Clads form angles of 45 degrees with shaft; terminations rounded. Surface flat from apex of cladome to clad termination. Upper half of cladome forms a smooth cone, rounded at the apex; lower portion of cladome between clads forms depressed-convex area. Chord 0.10 mm.; sagitta 0.12 mm.; length of shaft 0.50 mm.; diameter of shaft immediately below cladome 0.04 mm.

Univ. of Illinois, x-1470.

ANATETRAENE (g)

Plate 4, Fig. 15

Rhabdome gradually enlarges from termination to cladome. Clads gently curved throughout, making angles of 45 degrees or slightly less with shaft, rounded to pointed terminations. Upper surface of cladome smooth and rounded; cladome very broad. Surface of shaft and clads covered with very minute spines. Chord 0.06 mm.; sagitta 0.08 mm.; length of shaft 0.14 mm.; diameter of shaft 0.02 mm.

Remarks.—My collection contains only one specimen of spinose anatetraene.

Univ. of Illinois, x-1471.

ORTHODIAENES

Monaxons with two anteriorly directed clads at one end of the shaft.

ORTHODIAENE (a)

Plate 4, Fig. 9

Monaxons consisting of a straight shaft bearing two clads at one end. Shaft cylindrical, uniform in diameter. Clads short, emerging from shaft at angle of 85 to 90 degrees and increasing rapidly in broad smooth curve. Apex of cladome concave, lower than upper surface of clads; cladome broad. Length of clads 0.14 mm.; diameter of clads 0.08 mm.; length of shaft 0.44 mm.; diameter of shaft 0.05 mm.

Univ. of Illinois, x-1472.

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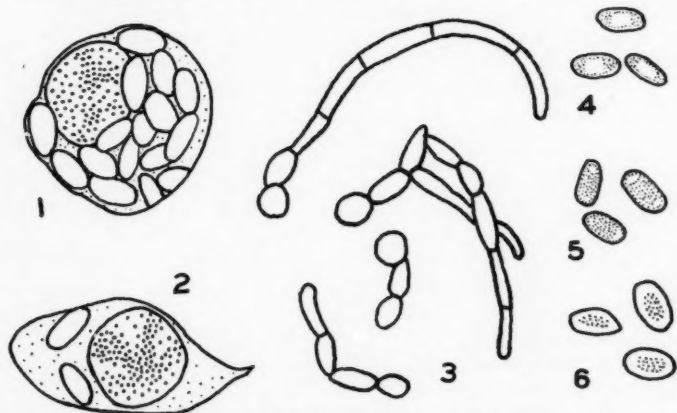
Phoma Stenobothri, a Fungus Parasite of the Grasshopper

Laurence R. Fitzgerald

During 1940, in the course of some work on the blood of the grasshopper *Melanoplus differentialis*, a number of peculiar, yeast-like cells were noted in the haemolymph and haemocytes of one of the animals under observation. Careful examination of other specimens from the same source (the colony maintained at the Zoology Department of the State University of Iowa) revealed four other grasshoppers that were similarly infected.

For some time after this, no additional animals were found to be infected, but nearly a year later a considerable number of animals was obtained with these parasites in the haemolymph, and several recurrences of the infection have been observed since.

The most noticeable characteristic of this infection is the presence in the haemolymph and haemocytes of small, bluntly ovoid cells $4.5\ \mu$ long and $1.5\text{--}2.5\ \mu$ wide (Figs. 1, 2, 4-6). These cells are extremely refractive, and this character, combined with their distinctive size and shape, allows them to be readily distinguished, even in fresh, unstained smears.



Text figs. 1-6. All the figures were drawn with the aid of a camera lucida, and are reproduced, with the exception of Fig. 3, at a magnification of 1750 diameters. Fig. 3 is reproduced at a magnification of 800 diameters.

1. Blood cell, showing numerous fungus cells within the cell membrane.—2. Same as fig. 1.—3. Hyphae and oidia from liquid culture.—4. Spores, stained by the Feulgen reaction.—5. Spores, stained heavily with haematoxylin.—6. Spores, stained with Giemsa's stain.

MATERIALS AND METHODS

The grasshoppers used in this study were all taken from the colony maintained at the Zoology Department of the State University of Iowa. Those being used for experimental purposes were kept in small cages which were autoclaved before each period of use. The diet fed the grasshoppers was that normally given to the animals in the colony. All experiments were set up with control groups, kept in the same room, under the same conditions, and with the same sex distribution. Before being used in experimental work the animals were taken from the colony and blood smears were made and examined on each of four successive days preceding the start of the experiment. If any of the animals in the lot showed signs of infection the entire group was discarded.

Injections were made with a 1.0 c.c. tuberculin syringe, equipped with a no. 26 needle. The needle was inserted between the intersegmental membranes on the ventral surface of the abdomen, lateral to the nerve cord. This method seemed to have no harmful effect on the animals, as these membranes are soft and easily penetrated. If the needle is run anteriorly and kept close to the body-wall, there is little danger of injuring any vital organ. The saline solution generally used in this laboratory for work with grasshoppers (Bodine, 1933) was used as the carrying medium for the injections.

The syringe mentioned above was also used in making blood-smears, a small quantity of saline being injected before the blood was withdrawn. Routine examinations were made with unstained preparations, but certain smears were fixed and stained as permanent preparations. Fixation by drying or heating was followed by either Wright's stain or Giemsa's stain, and fixation in Carnoy-Lebrun fluid was followed by either Giemsa's stain or the Feulgen reaction.

After death, each animal was opened along the ventral mid-line and the internal organs were examined under a binocular dissecting microscope. In certain cases, various organs were removed and fixed for sectioning. A number of animals were killed shortly before the expected time of death, examined in the usual way, and tissues were removed for microscopical study. These tissues were fixed in Bouin's fluid, sectioned and stained with either Heidenhain's or Regaud's haematoxylin or with Giemsa's stain.

Using the blood of infected grasshoppers as inoculum, serial dilution cultures were made. Several organisms were isolated from these cultures, but artificial inoculations, as described below, gave negative results for all but the one species here discussed.

INFECTION OF GRASSHOPPERS WITH SPORES GROWN ON ARTIFICIAL MEDIA

Spore suspensions were made up in sterile saline in the original culture tubes, poured into sterile, covered dishes, and injected with a tuberculin syringe as described above.

Of a group of fourteen grasshoppers injected with the spores of this organism, seven died within three days. The yeast-like cells were found in the

haemolymph and haemocytes, and in the period preceding their death the animals behaved as did those which had acquired the parasite naturally. Two others of this group showed the parasites in the blood for several days, but survived, and five showed no infection after the first day following the inoculation.

In an attempt to simulate the probable natural mode of infection, spores from cultures were smeared on lettuce, and then fed to groups of grasshoppers. Twelve animals were so treated. Two of these died within three days, after showing the yeast-like cells in their blood. Their behaviour and appearance, both external and internal, was typical of that of naturally infected animals. Six others showed yeast-like cells in their blood, but survived, while four others showed no sign of infection more than one day after the time of feeding.

These experiments strongly suggest that the organism which had been isolated was the causative organism of the disease originally observed, and that infection may occur through the eating of contaminated food. It is apparent, also, that a highly variable degree of resistance is present in the grasshoppers.

In spite of careful examination of serial sections of the alimentary tract of several grasshoppers, some of which had been infected by feeding experiments, the means by which the fungus passes through the wall of the alimentary canal could not be determined. It may be significant, though, that all of the diseased animals seen in the present work were also heavily parasitised by a protozoan, *Malpighamoeba locustae* King and Taylor (1936). These amoebae attack the walls of the Malpighian tubules causing numerous small lesions, and it is quite possible that the fungus cells enter the body cavity through these lesions.

DESCRIPTION OF THE FUNGUS ON ARTIFICIAL MEDIA

Several solid media were used in the attempts to obtain pure cultures of this fungus. The best results were secured with a weak synthetic medium having the following composition:

Glucose	10.0 gm.	MgSO ₄	0.25 gm.
Peptone	2.0 gm.	Agar agar	15.0 gm.
KH ₂ PO ₄	0.25 gm.	Distilled water	1000.0 c.c.

Typical growth, however, was also obtained on several other solid media, including Sabaroud's made up with glucose.

On this type of substrate, the fungus formed rather densely packed, dark brown, operculate pycnidia, about one-tenth of a millimeter or more in diameter (Plate 1, fig. 1). The spores were released from these pycnidia in small droplets of sticky fluid, which had a pinkish color at the time of release, but which became reddish on drying. The spores so released were ovoid, hyaline, very refractive, and were 4.5 μ long by 1.5-2.5 μ in width (Text—figs. 4, 5, 6).

White hyphae were widely scattered over the entire area of growth, and while not dense, were to be found in large numbers. The hyphae penetrating the sub-

strate formed a dense mat throughout the area of growth and were made up of cells averaging about $20\ \mu$ in length, and varying from $3.5\ \mu$ in width.

The liquid medium described by Hollande and Moreau (1923) was also used. This consists of a 2% peptone solution, containing 0.2% sodium chloride. Growth in this medium was of an altogether different nature from that found on the agar media used. Septate hyphae were formed, with cells varying from $20\text{--}30\ \mu$ in length and about $3\ \mu$ in width. These gave rise to numerous oidia, spherical in shape, with a diameter of approximately $4.5\ \mu$ which were often found in chains of several units (Text—fig. 3). The hyphae showed a tendency to form densely packed aggregates after several days of growth, with long hyphal portions radiating from a common center. It could not be determined whether all of the material in each of these aggregates was derived from a single hyphal fragment, or resulted from the entanglement of several hyphal portions.

THE FUNGUS IN THE GRASSHOPPER, AND ITS EFFECTS

The presence of this fungus in the grasshopper produces no external morphological changes in the animal, even at the time of death, and the changes following death consist only of the hardening and browning of the exoskeleton which normally follow death from a variety of causes in this species.

An animal that is seriously infected feeds little, if at all, and becomes more and more quiescent as the disease progresses. In the later stages the postural tonus of the animal is noticeably lowered, and movement of the limbs gradually ceases. This is first seen in the metathoracic legs, then in the mesothoracic legs, and finally in the prothoracic. The mouth parts seem to be capable of action even after all the legs have become immobile. The reason for the peculiar postero-anterior migration of this debility is not known, but it was observed in nearly all cases.

The internal organs show several important changes at the time of death. The alimentary tract is much darker than normal, as are the Malpighian tubules. The fat body is often tinged with a pinkish color, and commonly appears somewhat reduced in size. If the animal has been dead for an hour or more, the entire mass of viscera, except for the alimentary tract, is very fragile, and at the slightest touch gives off a milky fluid which when examined under the microscope, is found to consist of innumerable fungus cells mixed with cellular debris.

Fig. 1. Cross-section of two pycnidia.—Fig. 2. Cross-section of muscle from infected grasshopper. Three spindle-shaped fungus cells may be seen in the center of the section.—Fig. 3. Longitudinal section of muscle from an infected grasshopper. The breakdown of the tissue is shown in the lower part of the section. In the upper portion of the section, the striations may still be seen, but the fibers are beginning to separate.—Fig. 4. Cellular debris and fungus spores remaining after the complete breakdown of the muscle.—Fig. 5. The same, at a higher magnification.

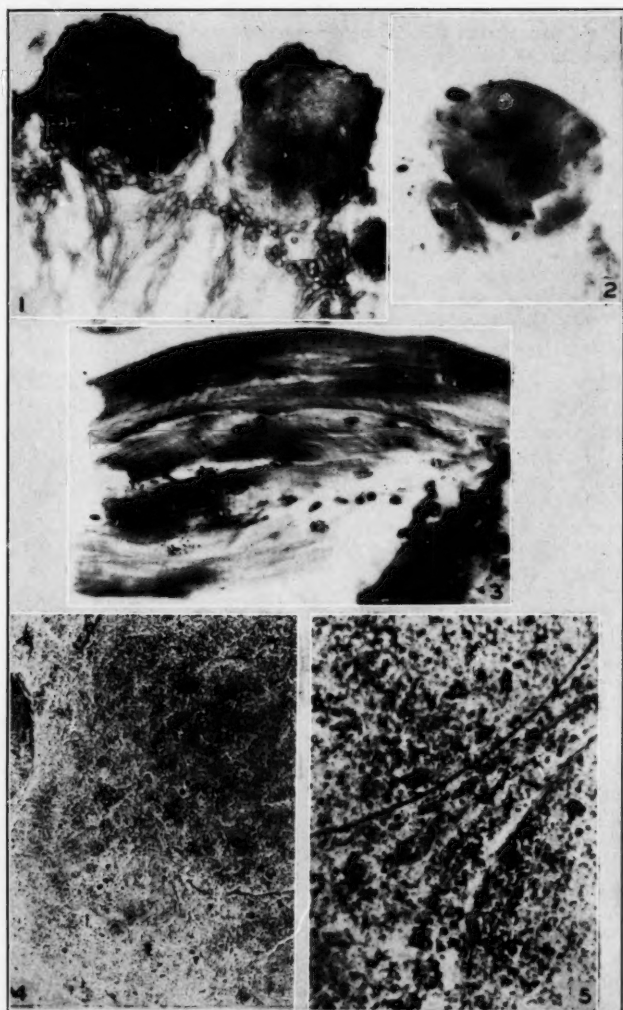


PLATE 1. All figures are from unretouched photomicrographs. Fig. 4 is reproduced at 80 diameters magnification, the others are all at 320 diameters magnification.

Histological examination of tissues taken from animals that are at the point of death reveals a rather surprising situation. As far as can be determined, the only tissues attacked before the death of the animal are the blood and the muscles.

The fungus cells first appear in the haemolymph, but the haemocytes are soon seen to contain many of these cells, probably as a result of phagocytosis (Text—figs. 1, 2). In the later stages of infection, all of the haemocytes contain the fungus cells. Since the number of blood cells appears to diminish during the progress of the disease and since they are often seen to be so packed with the fungus cells that the cell membrane is greatly stretched, it seems probable that some of the haemocytes are destroyed by the invaders.

The haemolymph shows changes in its macroscopic appearance as well. In the later stages of the infection, it seems to be slightly more viscous than normal, and has a decidedly milky appearance. This is especially noticeable in smears which are viewed with the naked eye in transmitted light.

The changes in the muscle are, perhaps, even more striking. The first thing noticed on microscopic examination of muscles from infected animals is that the fibers have become separated from each other, as do the fibrillae themselves. Almost simultaneously, the striations disappear from the tissue, and the material has the appearance of a number of disorganised fibers of uniform appearance (Plate 1, figs. 2, 3). This is followed by a complete breakdown of the cellular structure, and in sections of such tissue nothing but a mass of cellular debris closely packed with fungus cells is visible (Plate 1, figs. 4, 5).

This effect is shown earlier and to a greater extent by the skeletal muscles than by the visceral muscles. In fact, the skeletal muscles are usually seen to be in the last stages of disintegration at the time when the visceral muscles are just beginning to show the first signs of degeneration.

A careful search of the literature has revealed only one other report of a similar organism. In Uvarov's "Locusts and Grasshoppers" (1928) reference is made to a yeast-like parasite of several species of *Stenobothrus*, described by Hollande and Moreau (1923) as *Isaria Stenobothri*. A critical comparison of the organism reported here and the so-called *Isaria Stenobothri* indicates that they are the same. However, the characteristics of the fungus are such that it seems necessary to place it in the genus *Phoma* and to make the following new combination.

MYCOLOGICAL DESCRIPTION OF THE FUNGUS

Phoma Stenobothri (Hollande and Moreau) comb. nov.

Isaria stenobothri Hollande and Moreau, Arch. Zool. Exp. et Gen. 61: 59-74, 1923.

On solid media: pycnidia densely aggregated, subspherical, subcarbonous, distinctly operculate, lower half immersed in mycelium, upper half free, 100-

150 μ in diam., wall cells $20 \times 3 \mu$; whitish aerial mycelia present in older cultures; conidia borne singly, pinkish in mass, bluntly ovoid, biguttulate, hyaline, extremely refractive, $4.5 \times 1.5-2.5 \mu$. In liquid medium hyphae septate, cells $20-30 \times 3 \mu$; oidia spherical, 4.5μ diam., often in chains of from 3 to 5. In grasshopper, forming yeast-like cells in blood stream only, except following destruction in other tissues.

Hab. — From cultures obtained from blood of the grasshopper *Melanoplus differentialis* (Acrididae, Orthoptera).

SUMMARY

1. A fungus parasite of certain species of European grasshoppers originally described by Hollande and Moreau (1923) under the name of *Isaria Stenobothri*, has been found in a colony of *Melanoplus differentialis* maintained at the State University of Iowa.

2. The fungus taken from infected grasshoppers has been grown in pure culture on artificial media and the material so secured used to infect healthy grasshoppers.

3. The characteristics of this fungus are such that it seems necessary to place it in the genus *Phoma*, and, therefore, the new combination *Phoma Stenobothri* (Holl. and Mor.) is made.

The author is deeply indebted to Dr. E. H. Slifer of the Department of Zoology, and to Dr. G. W. Martin of the Department of Botany of the State University of Iowa, for their generous criticism and advice.

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Edward Palmer's Collections in Arizona in 1869, 1876, and 1877

Part I. General Discussion; Itinerary and Sources

Rogers McVaugh

Included in the recently published "Flowering Plants and Ferns of Arizona"¹ are some 30 species admitted to the Arizona flora on the basis of collections made by Edward Palmer in 1869, 1876 or 1877, but not otherwise known to occur in the state. Some of these species are admitted with expressed reservations because of the lack of knowledge concerning Palmer's collecting localities in the years in question; there is even the possibility that some of the specimens may have come from a region other than Arizona. Many of Palmer's collections of this period were distributed without definite locality-data, some of them bearing nothing more than his serial number and the general notation "Arizona" or "Southern Utah, Northern Arizona, etc." The Arizona collections of 1869, with few exceptions, bear no serial numbers, but in some cases have definite localities. The present paper is written in an attempt to set forth an account of Palmer's travels in the years under discussion, and to clarify the situation in regard to the doubtful collections cited by Kearney and Peebles.

The collection of plants made by Edward Palmer in 1869 was a large one, which was sent directly to Washington, Palmer having been employed as agricultural explorer jointly by the Department of Agriculture, the Smithsonian Institution, and the Army Medical Museum.² Unhappily the then botanist of the Department of Agriculture, C. C. Parry, to whom the collections were sent, seems not to have distributed or even labelled them. It is probable that they were left in storage, packed as sent in by Palmer, for several years. George Vasey, who succeeded Parry as botanist, ultimately performed the work of labeling the specimens, copying by hand the data which may be presumed to have accompanied Palmer's packages of plants. The doubt which has arisen in regard to the authenticity of the localities assigned by Vasey stems chiefly from two sources. In the first place, some of the specimens labelled "Arizona" represent species of known boreal affinities (for example, *Arctostaphylos uva-ursi*), which have not been found again in Arizona in spite of intensive collecting in the high mountains in recent years. In the second place, as pointed out by Safford some years ago,³ at least a part of the 1869 collection was lost at sea. It has been assumed by Williams⁴ and doubtless by others that the loss

¹ Flowering Plants and Ferns of Arizona, by Thomas H. Kearney, Robert H. Peebles, and Collaborators. U.S.D.A. Misc. Pub. 423. Washington, 1942.

² Report of the Commissioner of Agriculture for 1869: 93, 1870.

³ Popular Science Monthly 78:345. 1911.

⁴ Ann. Mo. Bot. Gard. 24:62. 1937.

was a great one, comprising essentially the entire year's collection and so raising the question of the authenticity of any specimen dated 1869.

Both the questions in the preceding paragraph can be answered, although at the present time the first one must be answered somewhat tentatively. It seems likely that the boreal, Rocky Mountain and plains species labelled as from Arizona came in reality from the Colorado-Nebraska region, where Palmer collected plants while serving as an Army surgeon during the Civil War. In April, 1862, his command left Leavenworth, Kansas, for Camp Weld, Colorado, traveling by way of Fort Kearney, Nebraska, and Julesburg, Colorado. He was stationed in Colorado until the following April, and during this time made approximately 165 collections of plants. He collected not only on the journeys to and from Colorado, but also in the high mountains near Denver during the summer of 1862. Apparently because of delays incident to the war, the specimens did not reach Washington until 1864, when their receipt was noted in the Annual Report of the Smithsonian Institution.⁵ The field notes pertaining to the specimens are preserved in the historical files of the Smithsonian, under Accession 291, but the specimens themselves seem to have disappeared without leaving any trace. Search through the National Herbarium and through lists of exsiccatae in various taxonomic papers fails to reveal any mention of collections made by Palmer in Colorado.

The most probable explanation seems to be that Colorado plants of 1862 were stored by the Smithsonian Institution until after the transfer of the herbarium to the Department of Agriculture in 1869; subsequently in some way they may have been confused by Vasey with the collections made in Arizona in 1869. That this is well within the bounds of possibility is evident when one considers Palmer's method of preparing his specimens; his usual procedure was to write out his field notes separately, packing the plants in bundles according to locality and sending the notes under separate cover. If his Colorado collections were not labelled or studied until 10 years or more after their collection, having endured in the meanwhile a delay of 2 years in transit, the field markings attached to the bundles may well have been effaced or lost.

It seems clear, moreover, that there was some confusion in Washington regarding the ultimate disposition of Palmer's collections of the period 1860-1864. Because of the lack of a practising botanist in Washington, Palmer requested that his plants be forwarded to St. Louis, to George Engelmann, for identification. It is probable that this was never done, and that the plants were lost until Vasey's time, when they were brought to light sometime after 1870. In a letter dated December 25, 1867 (now in the library of the Missouri Botanical Garden) Palmer wrote to Engelmann asking about his Colorado collections of "1860" (by 1860 I assume he meant 1862; in 1860 he did not reach Colorado until September or October and could not have made many collections). In the same letter he mentioned his specimens collected in 1863-64 between Fort Lyon, Colorado, and Fort Scott, Kansas, all of which he

⁵ Ann. Rep. Smiths. Inst. 1864: 87, 1865.

supposed had already been sent to St. Louis by the Smithsonian Institution. Apparently these never reached Engelmann, and probably they were never sent; scattered through the National Herbarium are Palmer collections of 1863 from Fort Lyon (see, for example, *Ann. Mo. Bot. Gard.* 17:366, 389; *Contr. U. S. Nat. Herb.* 7:167) and from Fort Scott (for example, *Eriogonum longifolium*), which seems to indicate that these, at least, were incorporated directly into the National Herbarium. Although at least some of the 1863 collections were made in duplicate and are known to have reached Torrey's hands (see *Ann. Mo. Bot. Gard.* 17:389), I can find no record indicating that any duplicate or other material was sent to Engelmann.

The second point mentioned above, that bearing on the loss by shipwreck of the 1869 collection, may be more or less satisfactorily settled by a consideration of Palmer's itinerary, in conjunction with specimens collected at certain definite localities during 1869. These localities, some of which are today almost forgotten, could scarcely have been invented by anyone writing Palmer's labels, and so must correspond to those actually visited by him. The details of his routes, as determined in other ways, agree well with those indicated by the localities on his specimens and, assuming that the herbarium labels are now associated with the plants for which they were originally intended, there seems no good reason to doubt the reliability of the locality-data found on the labels. It is probable that the loss by shipwreck was far less serious than has generally been supposed; this will be brought out more fully below.

Palmer left Washington on March 14, 1869. Traveling by way of Santa Fe, he reached Fort Wingate, New Mexico, on April 16th. From Fort Wingate, he visited the Navajo and other Indians, returning to the fort on May 1st and again about May 25th.⁶ About the first of June he joined a party led by officials of the Office of Indian Affairs, on a trip of about 3 weeks to the "Moqui" (Hopi) villages in Arizona; this trip was subsequently described by Vincent Colyer.⁷ The party went first to Fort Defiance, near the Arizona-New Mexico boundary, then "100 miles" west to the "Moquis," returning by way of Canyon de Chelly and Fort Defiance. The westernmost point reached was apparently the village of Oraibi, in western Navajo County, Arizona.

The events of the next 6 weeks are known only through Palmer's journal as quoted in an unpublished manuscript by W. E. Safford. On June 22nd, according to the journal, Palmer left Fort Wingate with an army escort, traveling by 6-mule wagon. On June 30th the detachment forded the Little Colorado River, and on July 4th they climbed the San Francisco Peak to the snow line. On July 9th they reached Fort Whipple, near Prescott, Arizona, where Palmer remained for nearly a month, leaving in the meanwhile for a trip to Bill Williams Mountain, with cavalry escort, on the 20th. The route taken is unknown to me, but Palmer's journal says that the camping place of the first night was at Preston's ranch, and that of the second night at Bean's Spring where "the surrounding country was strewn with blocks of volcanic rock." On

⁶ Palmer's letters to S. F. Baird, dated April 17, May 2, and May 31, all in historical files of the Smithsonian Institution, under Accession 1793.

⁷ Report of the Commissioner of Indian Affairs for 1870, app. C3.

July 30th, having made "a large collection" at Bill Williams Mountain and returned to his base at Fort Whipple, Palmer wrote to Joseph Henry from the fort in order to report progress.

Palmer's itinerary between July 30th and October 6th is not well known. Upon returning to Fort Whipple from Bill Williams Mountain he planned a trip to the "Astect" ruins at Camp Lincoln, some 50 miles east of Fort Whipple, and it is possible that the trip was made, for some of his collections are labelled as from Camp Lincoln (for example, *Euphorbia hyssopifolia*). Safford states that after the trip to Bill Williams Mountain Palmer travelled across country from Fort Whipple to Camp Mohave, thence down the Colorado River to the shipyard at Puerta Isabel, Sonora, where he collected invertebrates and other animals on both sides of the Gulf of California. Puerta Isabel was at the head of the Gulf, where its facilities served as a necessary adjunct to the then considerable river traffic to Yuma; with the cessation of this traffic, the yard was dismantled in 1878.⁸

On leaving Puerta Isabel (continuing Safford's account), Palmer proceeded up the Colorado to the mouth of the Gila River, thence up the Gila to the villages of the Pima Indians, continuing through Fort Whipple for a stay at Camp Date Creek to make further collections before leaving again for the Colorado River on September 16th. His route (still according to Safford) then followed the old Prescott-Ehrenberg stage road, via Date Creek, Cullen's Well, "Johnson's or Knapp's," Granite Wash, Hanniger Wells, and Tyson's Well 21 miles east of Ehrenberg. On reaching Ehrenberg at this time, Palmer sent his collections to San Francisco by steamer; here they were reshipped for Panama on board the "Golden City," which was subsequently lost at sea.

Palmer now appears to have made a second trip to Puerta Isabel; on October 6th he wrote to Joseph Henry from the "Mouth of the Colorado River," mentioning 2 boxes of specimens previously sent from La Paz⁹ and 3 boxes sent from his latest stopping place, whence he was writing. On October 18th he wrote again to Henry from the "Mouth of the Colorado River," having been delayed there but at the time of his letter planning to leave at once for Yuma, thence to proceed by coach to Tucson.¹⁰

Safford states that while at Tucson Palmer visited the nearby mission of San Xavier del Bac and also made a trip to Camp Bowie; I have not been able to substantiate either. On November 1st, according to Palmer's journal, he left Tucson by coach, bound for Guaymas, Sonora, by way of Altar and Hermosillo. He reached Guaymas about November 10th and left again on the 21st, taking passage on a small schooner plying between Guaymas and the Yaqui River. In three days he reached his destination, the ranch of Don José

⁸ Sykes, Godfrey. The Colorado Delta. Amer. Geog. Soc. Special Pub. no. 19, p. 34. 1937. The shipyard was located in a slough east of Philips Point, in approximate latitude 31° 48' N., longitude 114° 40' W.

⁹ La Paz was an old town some 7 miles upriver from Ehrenberg, one of the centers of shipping activities on the Colorado.

¹⁰ Palmer's letters to Joseph Henry, who was then the Secretary of the Smithsonian Institution, are to be found in the historical files of the Smithsonian under Accession 1793.

Maldonado, which lay about 10 miles inland from the mouth of the river. Here Palmer stayed two weeks. Then on December 8th he chartered a small boat to take him to Guaymas, which he reached on the 16th after having walked most of the distance along the shore, collecting as he went. About the end of December he left Guaymas for San Francisco on the steamer "Continental."

It seems clear that a very considerable proportion of the collections made in 1869 reached Washington in safety; Parry stated in his report for that year¹¹ that "the plants thus far received number about four hundred species." Probably all of the collections made in New Mexico and northeastern Arizona from April to June were sent overland from Fort Wingate before Palmer's departure for Fort Whipple, and apparently all reached Washington. The National Herbarium contains, in addition to specimens from Fort Wingate and Fort Defiance, plants which must have been collected in June or early July, on the trip between Fort Wingate and Fort Whipple. These last are from San Francisco Peak, from Bear Spring¹² and from Hell Canyon, Yavapai County, through which Palmer probably travelled on his way between San Francisco Peak and Prescott. There are also in the herbarium specimens from Bill Williams Mountain (for example, *Erigeron gulelmi* and *Pluchea camphorata*), from Fort Whipple, from Date Creek and, as mentioned above, from Camp Lincoln. Plants collected at Fort Whipple as late as August are known to have reached Washington; they are mentioned by Palmer in a letter to Engelmann the following year (letter dated November 19, 1870, in the library of the Missouri Botanical Garden). It is thus probable that Palmer's collections made enroute to, and near, Fort Whipple, in July and August, were not among those lost at sea.

When leaving Camp Date Creek for Ehrenberg, September 16th, Palmer wrote in his journal: "I took with me the collections I had made *since leaving Fort Whipple*" [*italics mine*]. The inference is that he sent from Ehrenberg, and so lost, all collections made during his first trip down the Colorado to Puerta Isabel¹³ and during his subsequent trip up the Gila and his stay at Camp Date Creek, as well as anything he may have collected about Ehrenberg or on the way there in September. The fate of the collections from the "mouth" of the Colorado River, mentioned in his letters of October 6th and 18th, is unknown, although Wheeler¹⁴ cites a specimen from "west of La Paz" which may have been collected on this trip. Subsequent collections, made at Guaymas, along the Yaqui River, and elsewhere in Sonora, reached Washington in

¹¹ Report of the Botanist in Rept. Comr. Agr. 1869:93. 1870.

¹² Probably about 4 miles northeast of the present site of Flagstaff, according to Barnes, Arizona Place Names, p. 41. Among the species so labelled is *Campanula parryi*, which in Arizona is a plant of high mountain meadows and so may well have been collected on the way up the San Francisco Peak.

¹³ It may be noted that there is no first-hand evidence that Palmer made more than one trip to Puerta Isabel; Safford's manuscript was written more than 30 years later, from Palmer's notes and recollections, and there is a possibility of some confusion with Palmer's trip of the following year, 1870, when he was again on the Colorado River and at Yuma in August.

¹⁴ *Rhodora* 43:140. 1941.

safety and are to be found in the National Herbarium; many of these, for some unknown reason, were assigned serial numbers.

Palmer's movements during his collecting trips of the years 1876 and 1877, in contrast to those of 1869, can readily be followed from day to day, chiefly through the medium of his own letters, approximately 70 of which are available to fix the details of his itinerary during this two-year period. His principal correspondents at this time were Baird, Vasey, Engelmann, D. C. Eaton, and F. W. Putnam. I am indebted to the authorities of the Smithsonian Institution, the Missouri Botanical Garden, the Library of Yale University, and the Peabody Museum for permission to study the letters in their keeping. In addition to the letters, there are available manuscript lists of Palmer's plant-collections during the years in question. These lists, prepared by Asa Gray, include the name, collector's number, and place of collection of each specimen, and have appended to them brief accounts of the collector's itineraries. Much supplemental information has been obtained from these lists, which have been made accessible through the kindness of the authorities of the Gray Herbarium. A third important source of information, for the 1877 trip only, is an article published by Scudder¹⁵ in 1878, in which dates and localities are given for many of Palmer's collections of butterflies.

Following is a summary of Palmer's travels in Arizona in 1876 and 1877:

1876

March 3 Arrived at Ehrenberg, Yuma County, by coach from San Bernardino, California. After a week's stay, he undertook a trip up the Colorado River by steamer.

March 11. Mouth of "Williams Fork" (Williams River or Bill Williams River), about 50 miles north of Ehrenberg.

March 15 (or 14). Arrived at the Colorado River Agency of the Mohave Reservation, between Williams Fork and Ehrenberg. This was presumably on the return trip from Williams Fork.

March ?23-April 6 or 7. Ehrenberg. Travelled by coach to Wickenburg, April 6th or 7th.

April ?8-?20. Wickenburg, Maricopa County.

April 22-May ?3. Prescott, Yavapai County. While at Prescott he collected at Walnut Grove (20 miles south of Prescott) and in the Juniper Mountains ("30 miles west of Prescott"). The location of the Juniper Mountains is in doubt, but it is probable that the name refers to the range which lies about 30 miles northwest, rather than west, of Prescott; it is also probable that Palmer collected here on the first day of his trip to Hardyville, which began about the first of May. The road from Prescott to Hardyville swung considerably to the northwest before turning southwest again to skirt the southern end of the Cerbat Mountains about where Kingman now stands.

May 4. Cottonwood Creek, "75 miles west of Prescott." Here, also, it seems

¹⁵ U. S. Geol. and Geogr. Surv. Bul. 4(1):253-258.

that "west" should read "northwest," and that Palmer's Cottonwood Creek is the White Cliff Creek which flows into the Big Sandy in T20N, R13W; there was in Palmer's time a station called Cottonwood in this vicinity.

The Gray manuscript list contains a single reference to a plant collected at "Willow Grove," and it may be that this specimen came from near Cottonwood Creek. Camp Willow Grove, an army camp from 1866 to 1869, was on the Prescott-Fort Mohave road in T21N, R12W.¹⁶

Safford states that Palmer's route led from Cottonwood Creek through "Hualpai Valley," this evidently refers to the pass north of the Hualpai Mountains, 25 or 30 miles west of Cottonwood Station.

May 6. "Cerat Mountain Pass, about 35 miles east of Hardyville." On this same day or the next he crossed Union Pass, in the Black Mountains about 25 miles west of Kingman, Mohave County.

May 8-12. Hardyville, Mohave County. Hardyville was on the Colorado River about 10 miles north of Fort Mohave. From here Palmer crossed the river into California and took the road across the desert to San Bernardino.

The Gray manuscript lists show that Palmer's Arizona collection of 1876 comprised 272 numbers, including 17 labelled only "Colorado Valley," and 56 vaguely designated as from "Wickenburg, etc." The remainder were distributed as follows:

Prescott	41	Colorado River Agency	
Cottonwood Creek	39	(including 1 from "Reserve")	10
Walnut Grove	24	Juniper Mountains	3
Ehrenberg	24	Cerat Mountains	2
Williams Fork	24	Willow Grove	1
Hardyville	20	Ehrenberg or Cottonwood Creek	1

The entire collection of 1876 comprised 649 numbered specimens and in addition several duplicate and supplementary numbers. The whole collection was arranged systematically before numbering; numbers 560-649 were arranged and numbered as a separate series which seems to have been sent to Engelmann for identification, the principal part of the collection (nos. 1-559) having been sent to Gray. Palmer sent the supplementary collection to Engelmann with a letter (December 13, 1876), giving the localities as follows: "Colorado River Valley Arizona March (are marked A) Hass-ay-ampa valley central Arizona . . . beginning of April (B) . . . Prescott Arizona mountain district central Arizona latter part of April (C) . . ." It appears that the 17 collections labelled by Gray "Colorado Valley" correspond with those sent to Engelmann and marked "A," if, as stated by Palmer, they were collected in March, they must have come from the very shores of the Colorado River, from the region between Ehrenberg and Williams Fork. The 56 collections designated by Gray as from "Wickenburg, etc.," must correspond with those from Hass-ay-ampa Valley marked "B" in Engelmann's set, and finally, the set marked "C," from Prescott, must correspond to the 10 specimens from Prescott enumerated by Gray in his list of numbers 560-649.

¹⁶ Barnes, Will C. *Arizona Place Names*, p. 489; see also the topographic map of the U.S.G.S., Diamond Creek Sheet.

1877

From January until late in June Palmer made his headquarters at St. George, Utah, during this time traveling out to points of interest in nearby Utah, Arizona, and Nevada.

April ?13-25. Trip from St. George to St. Thomas, Nevada, and return, passing through the corner of Arizona both coming and going. Collections were made at Beaver Dam (now Littlefield), on the Virgin River. According to Safford, Palmer also made collections at a place called Mesquite Flat, 12 miles from Beaver Dam.

April 27-May 4. Trip from St. George to Mokiak Pass and the Juniper Mountains (or Cedar Ridges), Arizona. None of these places appears on any map at my disposal, but in a letter to Engelmann (May 5, 1877) Palmer says he has just returned from "the broken mountains 75 miles E. of S. from St. George and not far from the Colorado River." Professor Walter P. Cottam of the University of Utah kindly informs me that Mokiak Pass lies on the road to Wolf Hole, about 40 miles south of St. George, and that the term "Juniper Mountains" in this case probably refers to the wooded ridges along Mokiak Canyon.

May ?28-June 4. Second trip to Mokiak Pass and the Juniper Mountains.

June ?7-15. Trip from St. George to Mt. Trumbull, Arizona, and return. Palmer's route to Mt. Trumbull is unknown, but doubtless lay along the old Mormon wagon road down the Hurricane ledge, the so-called Temple Road.¹⁷

Leaving St. George on June 22nd, Palmer went by easy stages to Salt Lake City, collecting plants and archaeological material at Red Creek (Paragonah) and Beaver City (Beaver) and from the surrounding mountains.

The Arizona collection of 1877, according to Gray's list, comprised 124 numbers, of which 71 were from Mokiak Pass, 27 from Mt. Trumbull, and 26 from Beaver Dam. The bulk of the 1877 collection, which comprised a total of 502 numbers (not including duplicate and supplementary numbers), originated in Utah.

Part 2. A Consideration of Some Palmer Collections Cited in the

"Flowering Plants and Ferns of Arizona"

Rogers McVaugh and Thomas H. Kearney

In the following paragraphs are discussed briefly the species admitted to the flora of Arizona on the basis of collections made by Palmer and alleged to have come from that state. In some cases, as will transpire, it seems to be necessary to exclude the species from the known flora of Arizona; in other cases we are able to substantiate the records.

¹⁷ Barnes, Will C. Arizona Place Names, p. 440.

Name	Name given by Gray	Palmer's Collection number	Locality According to Gray	Only Record for Arizona
1876				
<i>Astephanus ulahensis</i> Engelm.	same	440	Hardyville	
<i>Calycosotis parryi</i> A. Gray	same	292	Cottonwood Creek	
<i>Fagonia longipes</i> Standl. (TYPE)	<i>Fagonia californica</i>	58	Williams Fork	
<i>Gilia matthewsii</i> A. Gray	<i>Gilia schottii</i>	404, part	"Moj. R. & Cottonwood"	x
<i>Lesquerella arizonica</i> S. Wats. (TYPE)	<i>Vesicaria</i> 19	16	Juniper Mountains	
<i>Nemacladus gracilis</i> Eastw.	<i>Nemacladus ramosissimus</i>	300	None given	x
<i>Rorippa islandica</i> (Oeder) Borbás	<i>Nasturtium polustre</i>	563	Colorado Valley	x
<i>Thlaspi purpurascens</i> Rydb. (TYPE)	<i>Thlaspi alpestre</i>	571	None given	
1877				
<i>Aconitum glaberrimum</i> Rydb. (TYPE)	<i>Aconitum nasutum</i>	11	Beaver City, Utah	
<i>Angelica pinnata</i> S. Wats.	<i>Selinum kingii</i>	183	Red Creek (Paragonah), Utah	x
<i>Catoloba aquatica</i> (L.) Beauv.	same	486	Beaver City, Utah	x
<i>Centaurium exaltatum</i> (Griseb.) W. F. Wight	<i>Erythraea douglasii</i>	303	Beaver City, Utah	x
<i>Cleomella plocasperma</i> S. Wats.	<i>Cleomella angustifolia</i>	44	Beaver City, Utah	x
<i>Dodecatheon pauciflorum</i> (Dur.) Greene	<i>Dodecatheon media</i>	298	Beaver Valley, 20 Utah	x
<i>Laphania palmeri</i> A. Gray (TYPE)	<i>Laphania palmeri</i> n. sp.	199	Beaver Dam, Arizona	
<i>Petalonyx parryi</i> A. Gray	" <i>Petalonyx nitidus</i> (P. parryi)"	175	St. George, Utah	
<i>Potentilla rivalis</i> var. <i>millegiana</i> (Engelm.) S. Wats.	same	143	St. George, Utah	x
<i>Potentilla pectinisecla</i> Rydb.	<i>Potentilla gracilis</i> var. <i>flabelliformis</i>	145	Beaver Valley, 20 Utah	x
<i>Psathyrotes annua</i> (Nutt.) A. Gray	same	266	St. George, Utah	x
<i>Tetrameuris arizonica</i> Greene (TYPE)	<i>Actinella acutis</i>	259	Mt. Trumbull, Arizona	
<i>Townsendia arizonica</i> A. Gray (TYPE)	<i>Townsendia</i>?	204	Mt. Trumbull, Arizona	

19 The specific name used by Gray was never published in *Vesicaria*.

20 The locality as written by Gray is "Beaver Valley, near Red Creek." The topographic map (U.S.G.S., Utah, Kanab Sheet) indicates that the valley "near Red Creek" is Bear Valley, not Beaver. The map (first issued in 1886 and based chiefly on the Powell surveys) shows a road from the Parowan Valley, in which Paragonah ("Red Creek") lies, through Bear Valley and skirting Bear Valley Peak which lies but a few miles east of Paragonah.

Sixteen species are unknown from Arizona except through Palmer's collections dated 1869; this total includes 1 doubtful identification (*Eragrostis pectinacea*), one species known from the type only (*Erigeron perglaber*), one variety of a widespread species (*Agoseris glauca* var. *dasycephala*), and one species (*Morus grisea*) which is apparently but an exceptionally pubescent form of another and more widely ranging plant. Of the remaining 12 species two (*Cathastecum erectum* and *Euphorbia platysperma*) may well have been collected in southern Arizona.¹⁸ One species, *Mertensia arizonica*, may indeed have come from Arizona, since its known range includes southern Utah. Nine species seem, because of their known habitat preferences and geographical ranges, to be foreign to the flora of Arizona and are apparently to be excluded unless new localities at which they occur are discovered within the state: *Arctostaphylos uva-ursi*, *Arenaria congesta*, *Crepis acuminata*, *Helianthus subrhomboides*, *Lilium umbellatum*, *Lycopus lucidus*, *Mertensia palmeri* (*M. paniculata*), *Polygonum viviparum*, and *Thelypodium lilacinum*. It is suggestive, but of course not conclusive, that these species, with the possible exception of *Mertensia paniculata*, occur in the Colorado-Nebraska region where Palmer collected in 1862.

In addition to the above there may be mentioned a specimen of *Leucampyx newberryi*, collected by Palmer, supposed to have come from Arizona, and dated "1872" by Vasey. Since Palmer did not visit Arizona in 1872, the date is certainly erroneous. The species is not otherwise known from Arizona, but is also a native of the Colorado-New Mexico region; it is possible that it should be added to the list at the end of the preceding paragraph, as a plant to be excluded from the flora of Arizona.

In regard to the collections of 1876 and 1877 it is possible to be more specific, chiefly with the aid of the information contained in the manuscript lists at the Gray Herbarium. The accompanying table lists 21 species and varieties, 11 of which have been reported from Arizona only on the basis of Palmer's collections of 1876 and 1877. The remaining 10 were cited without definite locality in the "Flowering Plants and Ferns of Arizona," were erroneously cited as to locality, or were cited without collection number. In the table the plants are associated with the localities given by Gray; collection numbers have been supplied where necessary and, as an additional check on the identity of the numbered collections, the names of the species as given by Gray are included.

It will be seen that definite localities are established for all but three of the 1876 collections. Two of the latter, *Nemacladus gracilis* and *Gilia matthewsii*, can be but doubtfully members of the Arizona flora. The former probably should be excluded because of its known occurrence in the Mojave Desert and the fact that Palmer collected in that area immediately after leaving Arizona

¹⁸ Yet another species, *Jatropha canescens*, is known from Arizona only through an undated specimen in the Gray Herbarium, labelled "Dr. Palmer—Arizona"; if actually from Arizona, it may have been collected in 1869, somewhere near the Arizona-Sonora boundary. We are indebted to Dr. Lyman B. Smith for checking the information on this specimen.

and so could easily have found it there. The *Gilia* is probably also to be excluded, because of the likelihood that the part of no. 404 identified as *G. matthewsii* came from the Mojave River, California, rather than from Cottonwood Creek, Arizona.

It is also possible to establish definite localities for all the 1877 collections cited above, with the reservation that numbers 11, 175, 199, 204, 303 and 486 are not mentioned by the authors of the flora of Arizona, so that the specimens bearing these numbers are not certainly identical with those mentioned in that work. Number 11, however, was cited by Rydberg as the type of *Aconitum glaberrimum*, and number 199, according to Dr. Lyman B. Smith, is the only collection of *Laphamia palmeri* at the Gray Herbarium that is old enough to be regarded as the type. In addition it may be said that Gray's manuscript lists, from which the above numbers and localities were taken, in no case included more than a single species of any of the genera in question (*Catabrosa*, *Petalonyx*, *Laphamia*, *Townsendia* and *Centaurium*), so that it seems probable that the numbers are correctly applied.

With the establishment of definite localities for these collections, it becomes apparent that *Angelica pinnata*, *Catabrosa aquatica*, *Centaurium exaltatum*, *Cleomella plocasperma*, *Dodecatheon pauciflorum*, *Potentilla rivalis* var. *millegrana*, *Potentilla pectinisetia* and *Psathyrotes annua*²¹ are to be excluded from the known flora of Arizona. It now appears, also, that the type of *Aconitum glaberrimum*, and the specimen of *Petalonyx parryi* cited by Kearney and Peebles, were not collected in Arizona.

Finally it may be noted that the type of *Tetraneuris arizonica* Greene, erroneously said to have come from "Treadwell, Arizona," and a part of the original material of *Townsendia arizonica* A. Gray, said to have come from "Fort Trumbull," were both collected by Palmer at Mt. Trumbull in 1877. Gray did not designate any type for *Townsendia arizonica*, and his original locality citation read "Fort Trumbull, etc." His original sheet of the species, we are informed through the kindness of Dr. Smith, bears 2 collections from other localities in addition to Palmer's no. 204 of 1877, so that this number is not necessarily to be regarded as the type.

²¹ A fragmentary collection of this species, mounted on the National Herbarium sheet of no. 266 of the 1877 trip, purports to have been collected in Arizona by Palmer in 1869 but, like the other doubtful collections of that year, is hardly to be considered trustworthy evidence of the occurrence of this species in the state.

Notes on Wisconsin Grasses—III

Agrostis, *Calamagrostis*, *Calamovilfa*

L. H. Shinnars

Four species of *Agrostis* are found in Wisconsin, distinguishable as follows:

- Palea present, half as long as the lemma or longer; plants with rhizomes or stolons, old plants forming mats.
- Panicle (8-)10-24 cm. long, remaining open in fruit; plants with underground rhizomes; uppermost leaf blades of flowering culms 6-13 cm. long.....*A. gigantea*
- Panicle 3-8(-10) cm. long, becoming closed in fruit; plants with stolons, but not underground rhizomes; uppermost leaf blades of flowering culms 2-7 cm. long.*A. stolonifera*
- Palea absent, or less than a third as long as the lemma; plants without rhizomes or stolons, strictly tufted.
- Uppermost leaf blades of flowering culms 0.5-5.5 cm. long.*A. scabra*
- Uppermost leaf blades of flowering culms more than 5.5 cm. long.
- Lower panicle branches more than 8 cm. long.*A. scabra*
- Lower panicle branches 1.5-8.0 cm. long.*A. perennans*

Philipson in his recent revision of the British species of *Agrostis* states that the actual type of *Agrostis alba* L. was a figure of *Poa nemoralis* (Philipson, 1937, p. 91). He adopts the name *Agrostis gigantea* Roth, which gives the common Red-top a much more appropriate as well as legitimate designation. The familiar plant of Wisconsin, now abundantly naturalized and still commonly planted as a lawn and pasture grass, is *A. gigantea* var. *dispar* (Michx.) Philipson l. c. p. 93. When growing as a wild plant, it prefers somewhat moist soil, being especially common along ditches and on stream banks; but it also thrives in quite dry situations. Like the next species, it is subject to attack by nematode worms, though much more rarely. Such parasitized plants may have been the basis for records of *Agrostis tenuis* in Wisconsin; no collections of this species from Wisconsin have been seen.

Agrostis stolonifera L. is represented in Wisconsin only by the typical variety, *A. stolonifera* var. *stolonifera* (L.) Koch. This has also been known as *A. stolonifera* var. *compacta* and *A. stolonifera* var. *maritima*. The plant described as *A. palustris* in Hitchcock's *Manual* is probably this, at least in part, but that name properly belongs to *A. stolonifera* var. *palustris* (Huds.) Farwell. *A. stolonifera* is rarely planted unless unintentionally, through its occurrence in impure commercial seed. Consequently it is very uncommon as a wild plant, but has become established in a few places, on shores of lakes and streams, or in pastures, especially in alkaline soils. In recent years it has begun to appear as a weed in railroad yards, apparently finding the alkalinity of cinders an acceptable substitute for that of ordinary soil. The plant is easily recognizable in the field, having the appearance of a miniature version of *A. gigantea*, and forming dense mats which produce an abundance of low, small-panicked flowering culms.

The two remaining species are both native, though they have weedy tendencies. *A. scabra* Willd. is a common railroad weed, and in sandy areas may form solid stands in fallow or recently abandoned fields. Most of the characters used to separate this species from the more southern *A. hyemalis* (Walt.) BSP.—larger size, broader leaves, longer spikelets (2.3 mm. long, as against 1.2-2.0 mm. in *A. hyemalis*), scattered position of spikelets on the branchlets, and later flowering (cf. Fernald, 1933; Deam, 1940)—do not hold. All the Wisconsin material examined apparently belongs to a single species varying in size and leaf proportions according to habitat and season, with spikelets 1.6-3.5 mm. long, occasionally showing a distinct tendency to be clustered toward the tips of the branchlets, but usually scattered. The main flowering period in Wisconsin is from early June to mid July, but scattered clumps regularly continue in flower into September or October. Specimens rarely show whether the glumes are spreading or connivent in fruit. Consequently it is exceedingly difficult to separate the two species in the herbarium. Lacking field acquaintance with *A. hyemalis*, I am accepting the conclusions of Deam for Indiana, recognizing two species and calling all the Wisconsin plants *A. scabra*, even though some collections fall into the size range of *A. hyemalis*.

Agrostis perennans (Walt.) Tuckerm. is common in northern Wisconsin, where it can sometimes be found forming robust clumps half a meter tall in open sandy ground. Generally however it prefers somewhat damp shady ground, and may be a delicate plant only a decimeter high, with only one or two flowering culms, looking entirely different from the robust form of open ground. Southward it is largely confined to woodlands. It combines relatively short panicle branches with relatively long upper leaf blades, while *A. scabra* has long panicle branches and short upper leaf blades. Though there is overlap in the measurements for both parts, individuals of *perennans* robust enough to have panicle branches as long as in small plants of *scabra* also have correspondingly larger leaves which exceed the maximum for *scabra*, while individuals of *scabra* robust enough to have leaves as long as in small plants of *perennans* also have correspondingly long panicle branches exceeding the maximum for *perennans*. Hence it becomes possible to separate the two as in the above key. The main flowering period of *A. perennans* is in August and September, but as mentioned above, *A. scabra* regularly continues in flower through the summer and fall, so that flowering time is of no help in separating the two.

Calamagrostis is represented in Wisconsin by three species, distinguishable as follows:

Glumes 2.5-4.5 mm. long, acute, exceeding the lemma by less than 1 mm.; callus hairs about as long as the lemma or slightly shorter.

Lowest panicle branches reaching 3.5-7.0 cm. in length; glumes 2.5-4.0 mm. long; panicle loose and open, becoming closed only after the seeds have fallen.

Lowest panicle branches reaching 1.5-3.5 cm. in length (rarely 4 cm. in robust individuals, in which case the glumes are more than 4 mm. long); glumes 2.8-4.5 mm. long; panicle narrow and compact, somewhat open while in full

- flower, but quickly closing again. *C. neglecta*
 Glumes 4.4-6.4 mm. long, with slender acuminate tips exceeding the lemma by more
 than 1 mm.; callus hairs longer than the lemma. *C. epigeios*

Calamagrostis canadensis (Michx.) Beauv. is one of our most abundant native grasses, as might be expected in a glaciated region with a large proportion of undrained land. The plant is not restricted to marshy ground, however; it is quite weedy, and often spreads by its creeping rootstocks up ditch banks or onto filled ground. It is not unusual to find it growing in open woods, sometimes on hillsides where it is not at all marshy. Some authors have used the length of the callus hairs to separate this species from the next and *C. inexpansa*, the hairs being $\frac{3}{4}$ or more as long as the lemma in *C. canadensis*, and $\frac{2}{3}$ - $\frac{3}{4}$ as long in the other two. This seems to depend partly on the maturity of the spikelet, and is not a reliable diagnostic character. As pointed out below, a duplicate type specimen of *C. inexpansa* has callus hairs more than $\frac{3}{4}$ as long as the lemma.

Calamagrostis neglecta (Ehrh.) Gaertn., Mey. & Schreb. is much less common than *C. canadensis*, occurring chiefly in marshes around lakes or tamarack bogs. Occasionally it appears as an introduction in ditches along railroads, probably being brought in from the Dakotas, as are many of our railroad weeds. This species has generally been separated from *C. inexpansa* A. Gray on the basis of narrower, smooth leaves, shorter ligule, smaller size, and more northern range (cf. Stebbins, 1930; Hitchcock, 1935). It has not been possible to recognize two species in Wisconsin. The length of the ligule (which is generally so torn that its original size cannot be determined with certainty) varies greatly on the same plant, and between duplicates from the same locality. Leaf width ranges from 0.3 mm. to 4 mm. with no discernible break, most specimens falling somewhere between the extremes. Correlation of roughness with wideness is not consistent. Some of the broadest-leaved collections (from Bailey's Harbor, Door Co.) show both rough and completely smooth forms, and nearly all degrees of intermediacy are represented in the state. The three most narrow-leaved extremes which have been seen are from Madison, Dane County; Reeseville, Dodge County; and Town of Erin, Washington County—all in the southern quarter of the state instead of the extreme north as might be expected. I have not been able to distinguish Stebbins' varieties, three of which, described under two species, were reported from Wisconsin.

Typical *Calamagrostis inexpansa* according to Stebbins is known from only two collections: one from New York (the type), and one from Alberta. A duplicate of the type in the University of Wisconsin Herbarium has lower panicle branches up to 6.5 cm. long; the uppermost leaf blade (not well pressed) is about 3.5 mm. wide, strongly scabrous on both surfaces (as is characteristic of *C. canadensis*, with rather rare exceptions, and very often true of *C. neglecta*). The glumes are 4.0 to 4.4 mm. long, and the callus hairs are nearly or quite as long as the lemma. In general appearance the panicle is about midway between well-developed *C. canadensis* and *C. neglecta*. The type of *Calamagrostis inexpansa* is evidently intermediate between these

two species; in all probability it represents a hybrid between them. If this is the case, its peculiar distribution and rare occurrence are easily understandable. Such a hybrid might be found in Wisconsin, but has not so far been reported.

The European *Calamagrostis epigeios* (L.) Roth has been reported as established in Pierce and Green Counties, where it was planted for erosion control (Burcalow, 1941). It is worth noting that hybrids between *C. epigeios* and *C. neglecta* have been found in Europe (e.g., Kneucker, Gramineae Exsiccatae Lieferung XXI Nr. 630, from Russia; the label refers to description in Neuman, Sver. Flora, p. 771, 1901).

Two forms of *Calamovilfa longifolia* (Hook.) Scribn. are found in Wisconsin: the species proper, a rare native in the extreme northwestern part of the state in counties bordering the St. Croix and Mississippi Rivers, rarely adventive along railroads or roadsides elsewhere; and var. *magna* Scribn. & Merr., locally abundant on sand dunes and beaches along Lake Michigan. In Hitchcock's *Manual* the variety is characterized merely as having the panicle more open and spreading, which might seem inadequate grounds upon which to base a variety. Anyone who has seen *Calamovilfa longifolia* as it grows in South Dakota, however, will find it hard to believe that the Lake Michigan plant can belong to the same species, so utterly dissimilar is its appearance in the field. The Great Plains plant has the panicle 12-30 (-40) cm. long, with branches ascending or nearly erect; the spikelets usually white or greenish white; and sheaths usually glabrous, rarely pubescent. The Lake Michigan plant has the panicle usually 30-60 cm. long, the branches widely spreading, the lower often slightly reflexed at maturity; the spikelets usually purple; and the sheaths usually pubescent, rarely glabrous. None of the critical characters can always be relied upon in separating herbarium specimens of the two (which because of their size are generally represented by atypical small specimens), but var. *magna* is decidedly different, and its recognition is amply justified.

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Quercus Prinus Linnaeus

Ernest J. Palmer

In the November, 1942, number of the American Midland Naturalist¹ Cornelius H. Muller published a description of what he regards as a new species of *Quercus* of the series *Prinoideae*. The full and adequate Latin and English descriptions accompanied by a photographic plate of the type specimen give an excellent idea of the tree, which it is stated is confined to eastern Texas.

But on reading the description and explanatory notes it is surprising to find that the new species is compared throughout with the chestnut oak or rock chestnut oak of the northeastern United States (*Quercus montana* Willd.) and with the chinquapin oak (*Q. Muhlenbergii* Engelm.) from both of which it is clearly distinct—and not with the swamp chestnut oak, cow oak or basket oak of the southern coastal plain (*Q. Prinus* L., as now understood—*Q. Michauxii* Nutt.).

Sargent² was apparently the first to point out that while *Quercus Prinus* as described by Linnaeus was probably a composite species, his reference to Catesby's full-page plate which clearly portrays the plant later named *Quercus Michauxii* by Nuttall, made it necessary to restore Linnaeus' name to the tree of the coastal plain and of the southern lowlands and to take up the next available name—*Quercus montana* Willd.—for the chestnut oak of the northeastern United States. This change was made in the second edition of Sargent's Manual and it has since been accepted in a number of other publications, including Sudworth's Check List of 1937,³ in which the changes adopted in the use of these names were explained in footnotes.

Such name transfers are always confusing, and for this reason, as well as through lack of critical knowledge, many specimens of oaks of species with similar leaves are found under wrong names in herbaria and species are sometimes erroneously reported in local lists and floras. But so far as I am aware, there has been no confusion among recent authors or in recent manuals as to the distinctions between the chestnut oak of the north, the chinquapin oak, and the cow oak or basket oak of the southern coastal plain and lowland. The distinctions are made quite clear in the second edition of Sargent's Manual, in the seventh edition of Gray's Manual, Britton and Brown Illustrated Flora, Britton and Shafer Trees of North America, and in Small's Floras. In all of these works except Sargent's Manual and Small's new Manual of the South-eastern Flora the northern chestnut oak is named *Quercus Prinus* and the

¹ Vol. 28, p. 743-745, fig. 1. 1942.

² Rhodora, vol. 17, p. 40. 1915.

³ U. S. Dept. Agric., Miscel. Circular No. 92, p. 109. 1927.

southern tree *Q. Michauxii*. There are no inconsistencies, so far as I can see, between the descriptions of *Quercus Prinus* (where the name is used in its presently accepted sense) or *Q. Michauxii* with that given by Muller for his proposed *Q. Houstoniana*.

Muller gave the range of *Quercus Muhlenbergii* in some detail and he also mentioned the fact that *Quercus Prinus (montana)* centers in the Atlantic States and does not extend as far west as the Mississippi River. But the range of *Quercus Prinus* as now understood was not given, and it is worth while to clear up that point. The range so far as known is as follows: from southern New Jersey and Delaware along the coastal plain to central Florida and westward through the Gulf States to the Trinity River in eastern Texas, and with a northward extension in the Mississippi Valley and along the Wabash and Ohio rivers to southeastern Missouri, southern Illinois, Indiana and Ohio. It is obvious that this range includes that given for *Quercus Houstoniana*.

The Sabine River that forms the boundary between Louisiana and Texas is not a large stream in most of its course. The oak we are considering is found on both sides of the river, and it is scarcely probable that the trees on the opposite sides are of two species. Nor can I, after examining specimens from the entire range as given above and after a long acquaintance with the tree in the field, see any taxonomic or ecological grounds for separating the Texas tree from that found over a wide range in similar regions to the eastward. The range of *Quercus Prinus* is very similar to that of *Q. lyrata* with which it is often associated, and many other trees of the southeastern flora have approximately the same western limit of range.

Quercus Prinus is a handsome, striking and well-marked tree. It is uncommon or comparatively rare in many parts of the coastal plain and along the borders of its range, but in moist alluvial ground along streams it is often abundant and of great economic value for lumber. It is sometimes called swamp white oak or swamp chestnut oak or simply white oak by the lumbermen and country people, but over the greater part of its range it is well known as basket oak or cow oak, and I have never heard either of these names applied to either *Quercus montana* or to *Q. Muhlenbergii*.

The synonymy is in part as follows:

QUERCUS PRINUS Linnaeus, Sp. Pl., ed. 1, vol. 2, p. 995. 1753.

Quercus Prinus (palustris) Michaux, Hist. Chenes Amer., No. 5, t. 6. 1801.

Quercus Michauxii Nuttall, Gen. vol. 2, p. 215. 1818.

Quercus Prinus var. *Michauxii* Chapman, Fl., p. 424. 1860.

Quercus Houstoniana Muller, Amer. Midl. Nat. vol. 28, p. 743, fig. 1. 1942.

ARNOLD ARBORETUM,
JAMAICA PLAIN, MASS.

Notes on North American Plants. IV.

F. R. Fosberg

This paper presents geographic and nomenclatural notes on species of *Cecropia*, *Abronia*, *Portulaca*, *Loeflingia*, *Hedyotis*, and *Pseudelephantopus* in Idaho, Oklahoma, New Mexico, and the southeastern U.S. Herbarium abbreviations are (USNA), U. S. National Arboretum, and (USFS), U.S. Forest Service.

CECROPIA ADENOPUS Mart.

A specimen that seems to be this species was recently sent in from St. Cloud, Osceola Co., Florida, by Dora Z. Greene. Several unbranched plants from 12 to 20 feet tall were growing, evidently established, in rather low ground beside a ditch. They had been frozen back several times. Nothing is known of how this South American species happened to be introduced into Florida. The single leaf available is more deeply cut than is usual for the species, but some Brazilian specimens match it closely. This seems to be the first report of this genus from continental U.S. The rather fragmentary specimen is deposited in the herbarium of the U.S. National Arboretum (USNA).

ABRONIA MELLIFERA Dougl.

A specimen from Sunset Drive, out of Boise, Cedar Co., Idaho, June 9, 1942, F. A. MacFadden 25028 (USNA) is apparently the first record of *Abronia* from Idaho. Prof Ray J. Davis, who is preparing a flora of Idaho, has told me (conversation 1942) that he has not found this genus in the state and has seen no notice of it in the literature.

PORTULACA CORONATA Small, Bull. Torr. Club 23:126. 1896.

P. lanceolata Engelm. Bost. Journ. Nat. Hist. 6:154. 1850 (non Haworth, Misc. Nat. 142, 1803).

It has evidently not been sufficiently emphasized that the name *Portulaca lanceolata* Haw., validly published for a species now referred to *Anacampseros*, from South Africa, antedates Engelmann's name by 47 years. The only available name for *P. lanceolata* Engelm., a widespread and distinct species, is apparently *P. coronata* Small, applied to a plant originally described from the granite outcrops of Georgia (Little Stone Mt.), and since generally considered identical with *P. lanceolata*. The characters used by Small to separate the two are inconsequential. The plant of the Mesilla Valley, New Mexico, referred by me to *P. lanceolata* (Am. Midl. Nat. 23:587, 1940) is really *Trianthema portulacastrum* L.

LOEFLINGIA TEXANA Hook.

This inconspicuous plant, not included in Jeffs & Little's check list of the

plants of Oklahoma, may be reported on basis of *McMurry 1179a*, collected in a pasture 3 mi. n. of Fort Supply, Harper Co., in 1942 (USNA).

***Hedyotis michauxii* Fosberg, nom. nov.**

Houstonia serpyllifolia Michx. Fl. Bor. Am. 1: 85, 1803.

Hedyotis serpyllifolia T. & G., Fl. N. Am. 2: 39, 1841 (Not Poir. 1813).

Houstonia tenella Pursh, Fl. Am. Sept. 106, 1814 (not *Hedyotis tenella* Hochst., nor Miq. ex Hook. f.)

The above name is proposed since both of the specific epithets which have been applied to this blue-flowered Appalachian species are preoccupied in *Hedyotis*.

PSEUDELEPHANTOPUS SPICATUS (Juss.) Rohr.

Elephantopus spicatus Juss.

This pantropic weed has recently become established in Florida. A specimen from Hillsborough State Park, Hillsborough River, northern Hillsborough Co., April 8, 1942, collected by *O. E. Baynard* (USNA), furnished by courtesy of Dr. G. R. Fessenden, bears the information that 2 plants appeared as volunteers in a picnic ground. The following year the colony had increased to 50 individuals. It would be well to eradicate this undesirable immigrant before it becomes well established, as in many tropical countries it is a very persistent weed.

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A Fen in Northwestern Iowa

W. A. Anderson

For some years the writer has been studying the flora of an interesting springy area located in Silver Lake Township, Dickinson County, Iowa (Sect. 32 T. 100 N. R. XXXVIII W.). Though the area lies close to Silver Lake, a shallow body of water some two miles in length, it has no connection with the lake, but is saturated at all times by an extensive group of springs. The geological structure of this springy region and the mineral composition of the water was described by Carter (1939).

The following sixty-four species of Angiosperms have been collected and identified from the area. Identification has been facilitated and nomenclatorial problems simplified by use of Deam's Flora of Indiana, Fassett's Manual of Aquatic Plants and Hitchcock's Grasses of the United States. Twenty-nine of the sixty-four species in this list are plants of very specialized habitats, but of wide distribution. These are indicated in the list by the following symbols:

DM—Deam's Flora of Indiana—in marls.

DS—Deam's Flora—in springy places.

DB—Deam's Flora—in bogs.

H—Halophytes according to Svenson (1927).

Interesting plants not represented in these categories are marked by special notation.

Plants of Silver Lake Fen

<i>Allium canadense</i> L.	<i>Galium obtusum</i> Bigel.
<i>Aster novae-angliae</i> L.	<i>G. trifidum</i> L.—DB
<i>A. puniceus</i> L.	<i>Gentiana procera</i> Holm—DS
<i>Berula erecta</i> (Huds.) Coville ¹	<i>Gerardia purpurea</i> L.
<i>Calamagrostis inexpansa</i> Gray—DM	<i>Geum aleppicum</i> var. <i>strictum</i> (Ait.)
<i>Carex lanuginosa</i> Michx.	Fernald
<i>C. lurida</i> Wahl.	<i>Glyceria striata</i> (Lam.) Hitchc.
<i>C. rosea</i> Schkuhr	<i>Glycyrrhiza lepidota</i> (Nutt.) Pursh
<i>C. rostrata</i> Stokes	<i>Helenium autumnale</i> L.
<i>C. Sartwellii</i> Dewey—DM	<i>Hierochloa odorata</i> (L.) Beauv.—H
<i>C. aquatilis</i> Wahl. ²	<i>Hypoxis hirsuta</i> (L.) Coville—DM
<i>Cirsium altissimum</i> (L.) Spreng.	<i>Juncus brachycarpus</i> Engelm.
<i>Cuscuta glomerata</i> Choix.	<i>J. nodosus</i> L.—DM
<i>Cypripedium candidum</i> Muhl.—DS	<i>Liparis Loeselii</i> (L.) Richardson—DB
<i>Elymus canadensis</i> L.	<i>Lobelia Kalmi</i> L.—DM
<i>Epilobium densum</i> Raf.—DB	<i>L. siphilitica</i> L.
<i>Eupatorium perfoliatum</i> L.	<i>Lycopus asper</i> Greene
<i>E. maculatum</i> L.	<i>Lysimachia longifolia</i> Pursh—DS

¹ American Representatives of the Eurasian *Berula erecta* are segregated by Fernald (1942) as *B. pusilla* (Nutt.) Fernald.

² Swampy places—calcareous soils—Mackenzie (1935).

- Lysimachia thyrsiflora* L.
Parnassia glauca Raf.—DS-DM
Pedicularis lanceolata Michx.—DS
Phragmites communis Trin.—H
Potentilla Anserina L.—H
Pycnanthemum virginianum (L.) Durand
 and Jackson
Ranunculus Cymbalaria Pursh.—H
R. sceleratus L.
Ribes americanum Mill.—DS
Rosa suffulta Greene
Rhynchospora capillacea Torr.—DM-DS
Salix cordata Muhl.
Sanicula canadensis L.
Scirpus americanus Pers.—H
S. validus Vahl.—H
Scutellaria epilobiifolia Hamilton
Senecio aureus L.
Smilacina stellata (L.) Desf.
Solidago graminifolia (L.) Salisb.
S. Riddellii Frank.—DS-DM
Spartina pectinata Link.—H
Spiranthes cernua (L.) Richard—DM-DS
Thalictrum dasycarpum Fisch and Lall.—
 DS
Thaspium barbinode (Michx.) Nutt.
Triglochin maritima L.—H-DM
Typha latifolia L.
Utricularia macrorhiza LeConte
Viola nephrophylla Greene
Zigadenus glaucus Nutt.—DB

One of the chief difficulties in interpreting any floral area is in distinguishing the plants of real ecological or geographic significance from the others which grow with them. The writer has never seen an area nor visited a region which does not contain a mixture of floristic elements of one sort or another. Silver Lake Spring is no exception. The greater number of plants growing in it are species of moist prairie and pond margin elsewhere in the region.

Two environmental factors in the Silver Lake Spring which are immediately obvious are (1) low temperatures, at least in the spring centers, (2) high mineral content of the water. Limy concretions have been formed around the roots of plants, building up mounds of loosely consolidated lime and peat to a height of twenty feet above the level of Silver Lake. Through the generous assistance of Dr. A. B. Taylor of the University of Illinois measurements of acidity were made at a number of points. Temperatures (July 5, 1941) ranged from 8.5° C. in the spring centers to 31.5° C. in some open pools around the margins. The Beckman acidity meter gave readings from pH 6.79 to pH 8.05, with most of them falling between pH 7.00 and pH 7.30. Pools on the muck flats around the springs showed consistently higher pH values than did the spring centers, probably indicating increased mineral content by evaporation. Both low temperature and water rich in minerals may be necessary for the growth of some plant species found at Silver Lake, while other species respond to one factor and not to the other. *Triglochin maritima* is one of these. It seems to grow equally well in these Iowa springs and in the hot springs of Yellowstone National Park.

The occurrence of beds of calcareous peat or tufa in springy places is fairly common. There are remnants of several similar springy places in Dickinson County, Iowa, while twenty-five miles to the east, near Estherville, is an extensive area of the same sort, described by Wolden (1926). These areas are frequently referred to in American literature as "bogs." Gordon (1933) describes such a "bog" near Urbana, Ohio, saying further that "there is no reference in literature to bogs containing calcium." Metcalf and Griscom (1917) and Zenkert (1934) describe areas in New York with floristic composition similar to our Iowa "bog" while Steyermark (1938) reports a limy bog in

Missouri south of the glaciated region. In Europe Chouard (1922) describes two travertine-building springs in widely different parts of France, Blytt (1892) mentions tuff from lime-bearing springs in Sweden, while Halden (1934) includes "cupola" bogs in his classification of peat soils.

Svenson (l.c.) in accounting for widespread continental distribution of plants of brackish or calcareous habitats, says "at the time of recession of the ice sheet, a great area with homogeneous temperature and humidity must have extended along the front of the retreating ice with a terrain adapted to the growth of aquatic or semi-aquatic plants, and in alkaline regions to halophilous plants. Upon retreat of the ice cap, relics of the northern saline types would thus be left in mountainous regions about saline springs or in cold, calcareous bogs. A similar expansion of more southern halophytes and indifferent halophytes would naturally follow." Svenson thinks that many of these plants migrated from the West and ascribes part of the migration to human agencies. Human agencies seem unlikely as an explanation for the occurrence of such a highly localized group of plants as we have in the Silver Lake bog, especially as we find these same species repeated with few variations at Estherville, Iowa, in northern Indiana, at Urbana, Ohio, and in western New York. These plants of moist, calcareous habitats may have reached their wide distribution at the close of the last glacial period, but we do not have to account for their entire distribution at that time. Actually they have had ample opportunity to spread throughout the glaciated region during the long period of time from recession of the ice until the past century with its unprecedented disturbance of biological balance due to growth of modern agriculture. The vast number of kettleholes, ponds and sloughs which are scattered over the Wisconsin drift region have been, in the Middle West, much altered by farming operations, and yet, at present, we find more of Svenson's "indifferent halophytes" around the borders of such lakes and ponds than in the apparently specialized flora of Silver Lake bog. Shimek (1915) refers to springs of the Silver Lake type as "hillside bogs and seepy places," but finds only five species of wet ground plants which are distinctive of them. Although at present we do not find *Parnassia glauca* and *Triglochin maritima* around pond margins, it seems entirely possible that they may have grown in such places in the past, as a brief review of bog structure will show.

The structure of bogs or moors and their successional history is one of the oldest subjects of ecological research. Clements (1915) reviews a vast amount of literature relating to changes in post-pleistocene climate. Many papers cited by him describe peat deposits as having *Phragmites* or *Carex* peat, or else marl, at the bottom, even though they may be acid toward the surface and support a growth of *Sphagnum* with associated flora. More recent papers by Barnett (1937), Sears (1930, 1931), Hansen (1939) and Lane (1931) give similar pictures. Jewell and Brown (1929) describe an acid, *Sphagnum* bog in northern Michigan as growing around the margin of an alkaline pond, bringing about the transformation of the pond to a peat bog at the present time. *Sphagnum* bogs develop in regions of poor drainage if the climate is sufficiently

moist to leach out soluble minerals from upper soil layers. The process may be reversed, a *Sphagnum* bog being overgrown by *Calamagrostis* and *Cephalanthus* (Cain 1928).

The relations of these different types of peat formation are thoroughly discussed by Warming (1896), who designates alkaline peat-forming communities as *Sumpfmoores* or *Wiesenmoore* and acid-peat communities as *Sphagnummoore*. He gives a number of other German designations for each of these types.

Instead of calling all peat-forming communities, as at present, American ecologists would do well to use the English term "fen" for places where peat is deposited under alkaline conditions. In *Practical Plant Ecology*, p. 59, Tansley (1926) separates "marshland, fenland and mossland (moorland)" according as the soil is formed mainly by silt, by peat containing considerable quantities of these salts, or by peat poor in these salts. "Fen" is a term long applied to low lands along the estuaries of eastern England. In light of Tansley's clear statement it is not a local place name, but an equivalent of Warming's *Sumpfmoores*, equally applicable to similar plant communities wherever found. Tansley (l. c.) and Ashby, *et al.* (1938).

By this usage we have fens, both spring-fed and pond-margin, in northern Iowa. Pond-margin fens intergrade with marshes, according to the amount of silt deposited. There is considerable overlapping of species in all three. Of true bogs (*hochmoore*) we have very few, since the prairie climate is not favorable to the growth of *Sphagnum*. In moister climates many ponds are converted into bogs, often with fens as an intermediate stage. In such regions the last places to persist as fens are those with a continual influx of mineralized water, such as the springs at Urbana, Ohio, in southern Missouri, and in western New York, or along the estuaries of clear streams from limestone regions like those of eastern England.

Summary

1. A flora of a lime-bearing spring in northwestern Iowa is described.
2. The specialties in this flora belongs to a wide-ranging northern group of plants characteristic of marl deposits, springs or both. Some have been described as "indifferent halophytes."
3. The flora conforms to that of a *fen*, which term is suggested for use in America to designate alkaline peat formations.

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History and Orthography of the Celastraceous Genus "Pachystima" Rafinesque

Louis Cutter Wheeler

While browsing through the writings of Rafinesque looking for Euphorbiaceae which might never have been indexed it was noticed that Rafinesque spelled his generic name "Paxistima" and "Pachistima" rather than the commonly used "Pachystima." Also it was evident that the name was first published as a nomen nudum and, though *Ilex? myrsinites* Pursh was said to belong to the new genus, the transfer was not made and would have been ineffective if it had been attempted since a binomial in an undescribed genus is of no force.¹ Index Kewensis lists the transfer as having been made in the first publication. An inquiry into the validation of the genus and the formal transfer of a species to it was obviously needed. After much futile delving, Watson's "Bibliographic Index to North American Botany" supplied the clue. Checking the reference supplied by Watson revealed that when Rafinesque validated his genus he used the spelling "Paxistima" which must stand unless it is worth while to conserve an erroneous, though customary, spelling for a genus of but two or three species. The following bibliographic synopsis will present the evidence for the above statements.

PAXISTIMA Raf., *Sylva Telluriana*, 42. 1838, here amply described and the combination *P. myrsinites* (Pursh.) Raf. made; based on *Ilex? myrsinites* Pursh, which is consequently the type species of *Paxistima*. *Pachistima* Raf., *Amer. Mo. Mag.* 2(3):176. 1818, nomen nudum; op. cit., 4(3):191. 1819 (Jan.), nomen nudum; *Journ. Physique* 89:257. 1819 (July) nomen nudum; Endlicher, *Gen. Pl.*, 1089. 1840,² (as *Pachystima*) as synonym of *Oreophila* Nutt.; Endlicher, *Gen. Pl.*, 1424. 1841,³ based directly on *Oreophila* Nutt. ex. T. & G., *Fl. No. Amer.* 1:258. 1838⁴, not *Oreophila* D. Don, *Edinburgh Philos. Mag.* 11:388. 1832, and *Trans. Linn. Soc.* 16:178. 1833.

It appears that authors have accepted Rafinesque's earliest use of the generic name (a nomen nudum) or accepted Endlicher 1841. Apparently the first one who found Rafinesque's validation of 1838, and noted it, was S. Watson, *Smithsonian Misc. Coll.* 258:163. 1878 (*Bibliogr. Index No. Amer. Bot.*). Piper, *Contr. U. S. Nat. Herb.* 11:384. 1906 (*Fl. Wash.*) spells the name "*Pachistima*" as did Raf. in 1818 and 1819, though Piper does not mention any references of these dates. The spelling used by Piper may have been taken from Trelease in A. Gray, *Syn. Fl. No. Amer.* 1(1):397. 1897,

¹ International Rules of Botanical Nomenclature ed. 3, Art. 45. 1935.

² Date of publication according to A. Gray in copy at Gray Herbarium.

³ "Published after January, 1841." A. Gray in copy at Gray Herb.

⁴ Date according to Jackson, *Journ. Bot.* 31:298. 1893.

but is probable that Piper copied his reference (incorrectly) from Watson. Whatever the source, Piper cites "Fl. Tellur." instead of *Sylva Telluriana*, which is a gross error since these are two distinct works, and Piper makes no mention of the spelling "*Paxistima*" which he would have found if he had actually checked Watson's correctly given reference. It is possible that Jepson Fl. Calif. 2:450. 1936, copied the reference from Piper but used Endlicher's spelling.

Meisner, Pl. Vasc. Genera 2:348. 1843⁵ adds to the confusion by "correcting" the spelling to "*Pachystigma*" which is etymologically plausible, while as noted by Gray, Proc. Amer. Acad. Arts & Sci. 8:624. 1873, and Meehan, Proc. Acad. Nat. Sci. Philadelphia 1898:20. 1898, "*Pachystima*" is of dubious meaning, and "*Paxistima*" is even worse. However, names may be formed arbitrarily so long as they are pronounceable. Sprague, Kew Bull. Misc. Inform. 1928:364. 1928, has propounded the admirable principle that "In such cases as *Wisteria*, where opinions differ as to whether a name contains error or not, the original spelling should be retained." Instead of trying to rationalize the spelling, *Paxistima* should be spelled as in the first valid publication of the genus.

Ilex? myrsinites Pursh is a provisional name since not only was the question mark used to indicate doubt concerning its inclusion in *Ilex*, but Pursh stated: "I refer it to *Ilex* at present, till further observations, will decide to which genus it belongs, or whether it may not form one by itself." The following rule passed at the International Botanical Congress in 1935 requires, for valid publication, definite acceptance of a name by its author: "A name of a taxonomic group is not validly published unless it is definitely accepted by the author who publishes it. A name proposed provisionally (nomen provisorium) in anticipation of the eventual acceptance of the group, or merely mentioned incidentally is not validly published."⁶ Some authors dislike this rule especially when it affects a name which they have been using, but this dislike does not weaken the rule. — Nuttall, in renaming the species (under *Myginda*) may have done so because of the close similarity between *myrsinites* and [*Myginda*] *myrsinoides* [HBK].

The following species belong to the genus *Paxistima*. The names in each paragraph are all based on one type.

1. *Paxistima myrtifolia* (Nutt.) comb. nov.; based on *Myginda myrtifolia* Nutt., Gen. No. Amer. Pl. 1:109. 1818; based on the provisional *Ilex? myrsinites* Pursh, Fl. Amer. Sept. 1:119. 1814. *Oreophila myrtifolia* (Nutt.) Nutt. ex Torr. & Gray, Fl. No. Amer. 1:259. 1838.⁷ Type: "On the Rocky-mountains and near the Pacific Ocean. *M. Lewis*. ♀ July, Aug. v. s. in Herb.

⁵ Date given by Dalla Torre & Harms, Gen. Siphono., 290. 1900.

⁶ Zesde Internat. Bot. Congr. Proc. 1:365. 1936; see also Sprague, Journ. Bot. 74:75. 1936; and Wheeler, Rhodora 30:319. 1938, and Amer. Midl. Nat. 21:527-528. 1939, for discussion and examples.

⁷ Date according to Jackson, Journ. Bot. 31:298. 1893; Zoe 4:370. 1894.

Lewis." Two specimens are involved; both are on deposit at the Academy of Natural Sciences, Philadelphia, among the other Lewis & Clark Plants owned by the American Philosophical Society. The first specimen, with elliptic-oblongate leaves, bears the following data: "Rocky Mountains, June 16, 1806." To this label has been added, apparently in the hand of Thomas Meehan, "Pursh's copy of Lewis." According to Coues, Proc. Acad. Nat. Sci. Philadelphia 1898:296. 1898, this specimen was collected "On the Lo Lo Trail, vicinity of Hungry Creek of L. & C., a branch of the north fork of the south fork of the Kooskooskee River, next east of Collins' Creek." Piper, Contr. U. S. Nat. Herb. 11:384. 1906, states that "The exact spot in the Rocky Mountains is on the Lolo Trail near Hungry [Lolo] Creek, North Idaho." The second specimen, with very broad leaves, bears the following data: "A small shrub about 4 feet high with a deep purple berry, evergreen. Near the Pacific Ocean. Nov. 16th. 1805." According to Coues, l. c., this locality is "In camp on the Columbia in sight of the ocean, at the landward end of Haley's or Baker's Bay, just inside Chinook Point." No one has, to my knowledge, chosen either of these as type, but I infer that Piper intended to take the first, but probably merely because it was first mentioned. It should be left to the monographer to choose as type the specimen which seems to have supplied the more essential characters.

2. *PAXISTIMA MACROPHYLLA* Farr, Contr. Bot. Lab. Univ. Penn. 2: (3): 421. 1904, Type: Bear Creek, eastern slope of the Selkirk Mountains, British Columbia, altitude 3,670 feet, Aug. 20, 1904, *E. M. Farr* (hb. Univ. Penn. 37408). Large leaves, otherwise not distinctive.

3. *P. SCHAEFFERI* Farr, Ottawa Naturalist 20:108. 1906. Type: Bear Creek Station, Selkirk Mountains, British Columbia, May 25, 1905, *Mrs. Charles Schaffer* (a tag 512a on specimen, no number on label) (hb. Univ. Penn., s. n.). Apparently typical *P. myrtifolia*.

4. *P. KRAUTTERI* Farr, l. c. Type: Chaparral, 4,000 feet, Black Butte, Siskiyou County, California, July 15, 1905, *Louis Krautter* (hb. Univ. Penn. 42752). Narrow-leaved.

5. *P. CANBYI* A. Gray, Proc. Amer. Acad. Arts & Sci. 8:623. 1873.⁸ "Giles County, Virginia, on a bluff at "New River White Sulphur Springs," William M. Canby." (hb. Gray). Not seen, but there is no doubt about the interpretation of this species.

Two varieties have been described: *MYGINDA MYRTIFOLIA* Nutt. α MINOR Hooker, Fl. Bor.-Amer. 1:120, t. XLIA. 1830. This included the type of *Ilex? myrsinites* Pursh and may as well take the same type though some might protest. The plant illustrated agrees well with the first Lewis & Clark specimen cited above. — M. M. β MAJOR Hooker, l. c., fig. B. "Woods of Portage River, east side of the Rocky Mountains. Drummond." The type, presumably

⁸ Date confirmed by Ewan, Amer. Midl. Nat. 22:221. 1939.

somewhere in England if still extant, has not been examined. The figure agrees well with the second Lewis & Clark specimen cited above.

The first four species listed, and the two varieties, are all *Paxistima myrtifolia*, a widespread and a polymorphous species of the western United States and Canada. The fifth species, *P. canbyi*, is a restricted endemic of the eastern United States. There is probably a third (nameless) species in northern Mexico. Standley, Contr. U. S. Nat. Herb. 23:679. 1923 (Trees & Shrubs Mex.) indicates that the Mexican plant may be distinct from *P. myrsinites* to which he referred it. Recollection had it that there was a specimen of the Mexican plant in the U. S. National Herbarium but casual search in the summer of 1942 failed to locate it. There is a small specimen in Gray Herbarium, collected by Ed. Palmer, but it is wholly inadequate to serve as the basis of a new species.

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Notes and Discussion

Observations on *Ficimia streckeri* Taylor

Stanley and Dorothea Mulaik

In 1931 E. H. Taylor described *Ficimia streckeri* from a female taken near Rio Grande City, Texas. Additional specimens of this snake are now known from near the type area and to the southeast at Brownsville, Harlingen, and Edinburg in Texas and from Tuxpan in Vera Cruz.

This paper is a summary of variation within a series the authors secured in the Edinburg region. The largest number of specimens was secured during the spring and summer of 1935 in concrete canals. At that time government agencies made funds available to irrigation districts to keep the concrete canal banks clear of overhanging grass and weeds. Such cleaning up has since been discontinued, so that snakes can readily climb out after getting water.

When these snakes are kept in captivity in a box half filled with soil, they burrow with ease. On several occasions they escaped from snake-bags by crawling through a fairly tight overhand knot tied in the top.

Examination of the stomach contents of several specimens revealed that spiders constitute a large portion of the diet. They apparently did not feed on termites or other insects provided while in captivity.

In their review of the genus *Ficimia*,¹ Smith and Taylor establish two groups, based on differences in ranges and morphological characters, the genera *Cyalopion* and *Ficimia*. *Cyalopion* has 129 to 146 ventrals, and *Ficimia* 140 to 160. Our series of *Ficimia streckeri* has ventrals ranging from 128 to 150, which further bridges the gap between the genera.

In our series the head is no wider than the neck. The body is stout, cylindrical; the tail averages 14 per cent of the total length in males and 12 percent in females.

Scale rows are 19-17, occasionally 21-19-17 posterior to the first fourth of the body. There are no apical pits in the scales. Ventrals in males number 128 to 144, the caudals 35 to 40. In females the ventrals number 144 to 150 and the caudals 30 to 34. However the caudals divided by ventrals range from 0.256 to 0.298 with an average of 0.277 in males, while in females the range is 0.200 to 0.233 with an average of 0.215. These figures seem significant as indices of sex.

The anal plate is divided; supralabials 7-7; infralabials 8-8 or less often 7-7 or 7-8. The nasal plate is usually fused with the first labial and this scale is often entire, with the nostril placed near its center, or near its dorsal edge, but usually with a suture from the nostril dorsally, posteriorly, or more often toward the second labial. The eye borders

¹ Jour. Wash. Acad. Sci., vol. 31, no. 8, 1941.

The body and tail above is Storm Gray with 37 to 45 narrow Marble Green cross-bars on body about a scale wide, passing to about the fourth row of scales, and 11 to 16 less distinct bars or spots on the tail. The sides are lighter with scattered spots. The ventrals are tan to beige; this color involves the first row of scales. Over thirty specimens have been examined; the above figures are based largely upon the ten males and six females in the personal collection of the authors, and on several males and females in the collection of L. Irby Davis.

the third and fourth labials. No loreal is present: preoculars 1-1; postoculars 1-1 except SM 69, which has the supralabial fused to the postocular on the right side. Anterior temporals 1-1; posterior temporals usually 2-2. There are no internasals except in SM 56, a female with a distinct internasal on the right and one incompletely separated from the prefrontal on the left. The rostral borders broadly on the frontal.

The dentition is as follows: maxillary teeth 13; dentary teeth 15; palatine teeth 10; and pterygoid teeth 13. All the teeth rather stout.

The total length of specimens in the present series ranges from 115 to 325 mm. Excluding the two smallest specimens the average for the others is 264 mm.

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Rafinesque's Bat in Indiana

Charles M. Kirkpatrick

A student of mine, Clinton Conaway, apparently has collected the first Rafinesque's Bat (*Nycticeius humeralis* Rafinesque) to be taken in Indiana. The specimen, a male, was shot in Dearborn County the evening of May 24, 1942. Identification of the specimen was verified by Dr. W. H. Burt, University of Michigan Museum of Zoology. The skin is in the collection of the Purdue Wildlife Laboratory.

Dr. M. W. Lyon, Jr. (Amer. Mid. Nat. 17:85, 1936) suggested that Rafinesque's Bat doubtlessly occurred in Indiana since it had been collected as near as Chicago. He also pointed out that earlier authors had included this species in their hypothetical lists for the state, so its present discovery is not altogether unexpected.

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Correction

In my account of the moles of Texas [Amer. Midl. Nat. 27(2):380-386], I find that an error was made in recording the alveolar length of the maxillary tooth row in each of the races discussed. The measurements recorded are actually those of the alveolar length of the molar $\frac{1}{m}$ premolar series. This error in no way alters the general conclusions drawn, but anyone using the paper should in all instances interpret "alveolar length of maxillary tooth row" as alveolar length of the molar $\frac{1}{m}$ premolar series.—W. B. DAVIS, Texas Cooperative Wildlife Research Unit, College Station, Texas.

Book Reviews

JOHN RAY. By Charles E. Raven. New York: The Macmillan Company, Cambridge: at the University Press, 1942. xix + 502 pp. \$7.00.

What a great man was John Ray! Born near Braintree in Essex, son of a blacksmith, in 1671, Ray became one of the outstanding figures of the heroic age of English science. When he died, in 1705, he was mourned not alone as a great naturalist, but also as a rarely beautiful character, "our countryman, the excellent Mr. Ray." Ray, indeed, was the first really great English naturalist, and it is somewhat surprising that we have had to wait until this late date for a full-length study of his life and works. It has been worth waiting for in the present volume the Reverend Dr. Charles E. Raven, Master of Christ's College, has done Ray the justice so long overdue him.

There was hardly a field of natural history in which Ray did not do work of outstanding importance. This work was principally of a taxonomic kind, and in the history of science the work on which Ray's fame most broadly rests is the *Synopsis Animalium Quadrupedum et Serpentina Generis*, published in 1693. In this work, on the mammals and reptiles, Ray laid the foundations of systematic zoology. It was a volume which in its day exercised a considerable influence. It am not sure that Dr. Raven has been altogether wise in not more fully discussing the importance of this work in the history of zoology. It is probable that we shall hear more about it in Professor F. J. Cole's *History of Zoology* now being printed by Macmillan in England.

Ray's *Historia Plantarum Generalis*, the first volume of which was published in 1686 and the second in 1688, totalling 2,860 closely printed folio pages, summarized the whole of the botanical knowledge of the time. This great work was written in poverty, and in the turmoil of a household in the throes of caring for Ray's newly born twin daughters. It is a landmark in the history of scientific botany. Of Ray's distinguished and original works on birds, fishes, insects, palaeontology, geology, and philosophical biology, Dr. Raven gives most excellent accounts in his book, and it is unnecessary to mention them here.

It is of interest to note that Ray's *Collection of English Proverbs* first published in 1670 is still being reprinted, as is his altogether original *Collection of English Words*, first published in 1673, which represented the first serious attempts to gather and preserve the folk-speech and to distinguish the local dialects of English.

Those who would know more of Ray's activities now have Dr. Raven's meritorious book to turn to. The volume is not one, however, which readily lends itself to dipping, but it belongs to the class which must be read through from beginning to end—a very pleasant and enlightening experience, and an ennobling one, too, for at this distance of time the sterling quality of Ray's character, if anything, gains in power. He was, and will always remain, the kind of man whom one is the better for having known. It is a tribute to Dr. Raven's treatment of his subject that one is able to say that.

While there is an excellent index, there is unfortunately no bibliography, while the footnote references are given in a style all Dr. Raven's own. Date and place of publication are usually altogether omitted. In a footnote the reader is simply referred to "Bodenheimer," as if all the world were aware of the too obvious fact that "Bodenheimer" refers to the best history of entomology in existence. Quite in passing mention is made of "Pope's spiteful humour," but only a very knowledgeable reader would know that it was Walter Pope and not Alexander Pope whom Dr. Raven had in mind.

Concerning the actual merit of Robert Morison's botanical work I know very little, but it has always been my understanding that it was of a very high quality. Dr. Raven is somewhat contemptuous of it. Morison's was not a pleasing character, and he was most barbarously rude to the gentle John Ray, but if his work was as original as

eminent botanists have said it is, enthusiasm for Ray should not blind us to its merits.

Dr. Raven refers to the earliest of Ray's published experiments "the famous record of 'Experiments concerning the Motion of the Sap in Trees'" which appeared in the *Philosophical Transactions* in 1699. It may be of interest to mention here, what seems to have been commonly overlooked in this connection, namely, that Ray and Willughby were undoubtedly not original in carrying out these experiments, as Dr. Raven states, and furthermore, that when the Royal Society requested the authors to experiment "whether there be any circulation of the juice in vegetables as there is of blood in animals," it was Claude Perrault's communication to the Academie at Paris, in 1668, "De la Circulation de la Sève," that was the original source of all this interest.

Finally, Dr. Raven's suggestion that "two essays from Oxford"—to which, characteristically, he gives no reference—"signed L.P." are strongly asserted to be by Tancred Robinson, cannot be accepted for the reason that the author describes himself as a Master of Arts, whereas Robinson was a physician and never took an M.A. Moreover, Robinson stated quite clearly that he had supplied some of the material for the essays but was not the author of them. There is not the slightest reason to believe that he was not wholly speaking the truth.

Faithborne's portrait of Ray is reproduced as frontispiece, the choice was a wise one, for the portrait is much more attractive than Mary Beale's painting now in the British Museum (Natural History).

Dr. Raven has put us all deeply in his debt for having given us such an admirable history of John Ray and his work. It remains but to add that the Cambridge University Press has produced the book in the usual good taste, and consummate presswork, which has come to be associated with its name.—M. F. ASHLEY MONTAGU, Department of Anatomy, Hahnemann Medical College and Hospital, Philadelphia, Pennsylvania.

TEXT-BOOK OF COMPARATIVE HISTOLOGY. By Elbert C. Cole. The Blakiston Company, Philadelphia, 1941. vii + 396 pp. 297 figs. \$4.00.

The study of the microscopic anatomy of man in conjunction with his gross anatomy is well-established and its value is generally appreciated. Not so generally, however, is adequate consideration given to the histology of the other vertebrates and the invertebrates; and because of this situation, the appearance of this book will undoubtedly be gratifying to many.

There are four sections: the first deals with histology as a subject of study, the nature and activities of cells, and the embryonic origin of tissues; the second portion is devoted to the general histology of tissues; the third constitutes a survey of the special histology of the various systems; and the last describes the instruments and techniques used in histological investigations.

The histological structures of tissues and organs of invertebrates as well as vertebrates are described. Even though most of the space is devoted to the vertebrates, the treatment of these animals may be considered too brief by some. In the reviewer's opinion, however, the book does not fail to come up to the author's intention—"a student handbook rather than a reference book." In many instances the brevity of treatment is offset by the references at the end of the chapters, references which should be employed by the instructor for supplementary information.

The section dealing with "Instruments and Methods" is a valuable one. The descriptions of the techniques and the diagrams which accompany them, because of their clarity and conciseness, will be helpful to both the instructor and the student.

The chief fault of the book lies in the illustrations. The author uses photomicrographs "freely... so that the student may become familiar with tissues as they appear in actual histological preparations." Unfortunately, many of the photomicrographs are so poor (or they were reproduced so poorly) that the writer cannot agree that they serve any purpose at all. Others which are rather good are not exploited to their fullest. More

complete labelling, indications of magnifications on the illustrations, and substitution of drawings for some of the photomicrographs would have improved the book's value as a "student handbook."

It is the reviewer's belief that the text is adequate; it can be used profitably not only in courses in histology but also for reference in other courses, such as comparative anatomy and laboratory technique.—E. LAWRENCE POWERS, JR.

GENERAL ZOOLOGY. By Tracy I. Storer. McGraw-Hill Book Company, New York, 1943 xii + 798 pp., 551 figs., 5 colored pls. \$3.75.

BIOLOGY, THE SCIENCE OF LIFE. By Mary Stuart MacDougall in collaboration with Robert Hegner. McGraw-Hill Book Company, New York, 1943. x + 963 pp., 555 figs. \$4.00.

These books represent contrasting and to some extent conflicting tendencies in college biology. One carries on the tradition of two separate sciences which are to be studied primarily upon a systematic basis. The other reflects an effort to combine two fields into a unified whole, primarily for the good of students whose formal contact with the life sciences may be limited to one year of instruction. On a more practical level, this second plan should prepare those students to teach the unified courses which are now the rule in high schools.

After an introductory statement, Professor Storer seeks to orient his readers by means of a 27-page chapter on the frog as a representative animal. This is followed by chapters on protoplasm, cells and tissues, organs and systems, reproduction and development (with modern diagrams showing the origin of mesoderm), genetics, ecology, evolution, biologic history and classifications. Filling 254 compact pages, this first part in itself is a comprehensive survey of zoologic principles and related material. Part II (485 pages) is devoted to a survey of animal phyla, with nine chapters on chordates and three on arthropods. Trochelminths, brachiopods, bryozoans and a few other minor phyla are crowded into a single chapter.

Doctors MacDougall and Hegner begin by contrasting living and lifeless matter, after which they deal with chemical compounds, protoplasm, cells, tissues and organs, ecology and classification. Part II (pages 97-222) is devoted to plant biology, with six chapters on the morphology and physiology of seed plants and three on major plant groups. Part III, on animals, parallels Part II of Storer's book plus the chapter on the frog; Part IV, dealing with foods, nutrition, circulation, reproduction and kindred topics gives much emphasis to man. Two remaining parts deal with germ cells, heredity and variation, adaptation, evolution, biology in human welfare and conservation.

One contrasts these books to the advantage of the former. Professor Storer's systematic chapters are more informative than those of MacDougall and Hegner, while his discussions of ecology, distribution, evolution and the history of zoology are more substantial and stimulating. But both books avoid subjects which, in this reviewer's experience, are vastly stimulating to novices. One of these is the origin of protein compounds and life—a subject vitalized though not settled by Baly and Oparin. Another is inadequacy of two traditional kingdoms, with the vistas of progress and clarification opened up by modern systems such as the four kingdoms advocated by Copeland. More could have been done to link fossils and fossil groups with living organisms and to develop descent diagrams that would organize the ideas of students. Such material is bound to involve speculation, which both volumes seek to avoid. But so long as speculation is reasonable and scientific it can do no great harm. Its value in stimulation and clarification of oft-confused ideas will outweigh many small disadvantages.—CARROLL LANE FENTON.

THE OSTRACODS OF ILLINOIS: Their Biology and Taxonomy. By C. Clayton Hoff. Illinois Biological Monographs 19(1-2):1-196, 8 plates. University of Illinois Press, Urbana, Illinois, 1942. \$2.50.

Hardly any common group of important animals has been more neglected on this continent than has the Ostracoda and Dr. Hoff has rendered a substantial biological service in his treatment of the biology and taxonomy of the 39 species recorded from Illinois. The first work on North American ostracods seems to have been done by Halde- man in 1841. More significant was the work of Herrick, Turner, Sharpe, Chambers and Forbes in the last three decades of the 19th century, particularly that of Turner and Sharpe. In the early part of the 20th century there have been many minor contributions, while particularly notable work was done by Sharpe for the U. S. National Museum and for Ward and Whipple's *Freshwater Biology*, by Furtos for Ohio, Massachusetts, Florida, North Carolina and the region of Yucatan, and by Dobbin for the Northwest coast. For comprehensive treatment of the biology of ostracods, Dr. Hoff points out, one must still rely upon the German "Handbuch der Zoologie" of Kuekenenthal-Krumbach and Klie's volume in the "Biologie der Tiere Deutschlands."

From a study of 713 field collections from all parts of the State, Hoff has raised the number of free-living species in Illinois from the 22 of Sharpe to 39, 11 of the 17 additions being described as new. The keys and descriptions of species with discussions of individual taxonomic and specific ecology constitute the greater part of the report (pp. 49-106).

Particularly interesting to the general or non-specialist reader is the account of the biology and morphology of the group (pp. 21-49). Methods of collecting, staining and preservation are given.

"If sufficient search is made," says the author, "there will be found scarcely a single kind of aquatic habitat in which ostracods are not found"; "independent factors such as type of bottom, current, and associated vegetation determine only to a minor degree the distribution of most species." Nevertheless, certain species can be classified as preferring temporary pools, permanent still waters, temporary running waters or permanent streams: "The sum total of the factors which are expressed in the four types of habitats mentioned appears to determine to a large degree, and with few exceptions, the species of ostracods present." Thus, temporary still water is considered characteristic for 5 species and 4 of these were found only in such waters. Six species were found only in permanent still waters and one generally in such a habitat. Two appeared only in temporary running waters, one only in permanent running water and one only in temporary or permanent running water; 15 species were less restricted and a few of these were notably indiscriminate as to the types of habitat considered. Eight species recorded by Sharpe were not encountered by Hoff, doubtless because of their local or seasonal distribution or their rarity. In all, 13 species were found only where there was no current (but 7 of these were found only once or twice.) Eleven were found predominantly in still water, 2 only where there was current, 4 predominantly in current. One species seems to have been indifferent: it was found 35 times in still water and 35 times in flowing water, and 14 of the records were in strong currents. Many of those living in substantial current show adaptations of the antennae for creeping rather than for swimming, with other presumed adaptive modifications of the shell.

Many species are intolerant of strongly acid waters but many others are tolerant of acid conditions and these generally have small shells with heavy organic covering. Physical factors other than current and hydrogen-ion concentration seem to have little effect.

The author disagrees with some but agrees with others as to the insignificance of freshwater ostracods as plankters, although they occasionally occur adventitiously in the plankton. No relation to particular associations of plants could be found, nor were there particular associations of species of ostracods other than such as were incidental to their relations to the four kinds of habitats previously mentioned. The writer does see some evidence of protective coloration among species which usually live among aquatic plants.

Hoff recognizes that his data with regard to seasonal distribution are limited but, by taking also into consideration the records of Sharpe, there are indications that certain species are found typically in the early vernal and aestival seasons; these include a number of species of *Candona*, but not all, and two species of *Cypricercus*. Two species of *Cypria*, one of *Physocyprya* and one of *Cypridorus* occurred throughout the period of the investigation, March to August, or through most of it; two or three species seemed to occur all the summer; only a few seem to pass the winter in the adult stage.

Except for the work by Turner, nothing has been done on the life histories and reproduction of American species, but a good deal has been done on European ostracods. The egg hatches into a shelled nauplius with the usual three appendages and in all there are nine instars including the sexually mature animals. Appendages increase in number and change in form and the shell also becomes altered in shape in various instars. The young have often been described as new species.

In seven species, for which males are unknown, reproduction seems always to be parthenogenetic. For five species males are occasionally found and reproduction is presumed to be ordinarily parthenogenetic. For two species, in which males are more abundant, reproduction is presumed to be both parthenogenetic and syngamic. For the great number of Illinois species males are always present and reproduction is thought to be syngamic. The fact that males of *Cyprinolus incongruens* have been found rarely in Germany, more frequently in Hungary and Bohemia, and in equal abundance with the females in North Africa, suggests that the mode of reproduction of different species may differ in different localities. No definite alternation of periods of syngamic and parthenogenetic reproduction, such as is known for Cladocera and some other organisms, has been shown for ostracods.

"All the ostracods in Illinois are oviparous except *Darwinula stephensoni* which retains the eggs during development in the posterior dorsal part of the shell cavity." The eggs of other species are usually attached to some substratum, especially plants, where they may undergo development at once or where they may remain, as in temporary ponds, to survive a period of drought or freezing. The number of generations per year varies from one, for certain species living in temporary waters, to many; but the number of generations and the length of life-span have not been investigated for American species.

Most species feed on bacteria and other minute organisms as well as on detritus. Some have mandibles adapted to rasping material from larger solid bodies and some of the larger species are said to feed on the bodies of dead animals.

With respect to distribution, certain species from Illinois have been found only in the Chicago region and others only in the southern portion of the State. As regards world distribution, we have the extremes represented by twelve species found as yet only in Illinois and one which is reported from all over the world except Australia. Others are known, respectively, only from the central United States, the United States, North America, Europe and North America, holarctic regions or holarctic and South America.

The author treats the ostracods as an order, subdivided into four suborders, only one of which, the suborder *Podocopa s. str.*, includes freshwater species. Of the four families recognized in the sub-order, one is strictly marine, one entirely freshwater and represented by only one species in Illinois; of the other two families one is chiefly marine, with three species found in Illinois, and the other, the *Cypridae*, common in both marine and freshwaters.

Appended are a good bibliography, nine plates, including 141 clear line drawings, and a good index.

Dr. Hoff has rendered distinct service, not only in this significant contribution to knowledge of American freshwater ostracods, but also in pointing out the inadequacies of our knowledge of the group and the opportunities for further research. The volume is a credit to the series of Illinois Biological Monographs and to the University of Illinois Press.—R. E. COKER, University of North Carolina, Chapel Hill, N. C.

RIO MAYO PLANTS. A Study of the Flora and Vegetation of the Valley of the Rio Mayo, Sonora. By Howard Scott Gentry. (With Foreword by Forrest Shreve). Carnegie Institution of Washington Publication 527. The Lord Baltimore Press, Baltimore, Md. The Meriden Gravure Company, Meriden, Conn. 1942. vii + 328 pp., 29 pls., 2 maps, 6 figs. \$2.25, paper cover; \$2.75, cloth binding.

This is one of those surprising books which, upon first glance gives one a "let down" feeling, but which, upon reading, reveals a wealth of information clearly presented. It improves with study. It contains data about the plants of the Rio Mayo drainage system, the uses to which they are put, and about the people who live among them and utilize them in the simple economy of the Indian and peon. The feeling of disappointment, soon dispelled, is probably felt only by the taxonomist who would have liked to see keys to the genera and species included. That feeling is largely displaced, however, when he finds that Mr. Gentry has written about the vegetation and floral relationships of the plants growing over some 6800 square miles of the "barranca region" of southeastern Sonora and adjacent Chihuahua—an area practically unknown botanically prior to Mr. Gentry's nearly two years of field work.

The book is divided into two parts, Part One dealing with the physical conditions encountered, descriptions of the vegetation, a report on several plant censuses, a gazeteer, successions in abandoned milpas, lists of cultivated plants grown in the area, and another list of the uses to which native plants are put.

Part Two is an annotated list of the species discovered in the Rio Mayo area, together with data on the type localities, range of the species in and adjacent to the Rio Mayo region, habitats, locality and collection numbers of the specimens cited, and varied comments on a number of anthropological, ecological and ethnobotanical features of the area. Much of this information could have been gleaned only by one possessing a thorough knowledge of Spanish and of the Indian dialects, and by one who was thoroughly sympathetic with, and acceptable among the inhabitants.

Following the annotated list is an enumeration of the eight new species, one new variety, and seven new combinations published in the book. Sixty-six new species or varieties based on specimens collected by Mr. Gentry but described by other authors are listed also.

Mr. Gentry has done a good piece of work in delimiting the four vegetational complexes which he calls: (1) Thorn Forest, roughly corresponding to the Lower Sonoran Zone; (2) Short Tree Forest, similar to the Subtropical Zone; (3) Oak Forest, roughly corresponding to the Upper Sonoran Zone; and (4) Pine Forest, which contains elements of both Transition and Canadian Zones. Among these, the densest cover, as measured by the number of individual plants per acre, occurs in the Thorn Forest, the sparsest in the upper parts of the Pine Forest. Elevations extend from near sea level to about 9,000 feet higher.

With all of its excellence, there are a few points, which seem to the reviewer, might have been improved. The half tones are, in some instances, lacking in depth and definition, probably because they were "blown up" from small negatives. I am at a loss, also, for a valid reason for devoting over thirty pages to a repetition of the list of annotated species to give the herbaria in which specimens are deposited. Why could not the appropriate abbreviations have been incorporated in the general annotated list? Some of the names listed in the gazeteer are located indefinitely and are valuable chiefly for the anthropological and ethnobotanical notes accompanying them. One error in the use of abbreviations for measurements occurs on page 31 where the leaf of *Conzattia sericea* is said to "... spread over an area of nearly half a square meter." Then in the following sentence, "The entire leaf is about 45 by 75 dm. in size, ..." The "dm." should have been "cm."

The outstanding feature of the book is its wealth of information about a little-known area. The notes on flower color, habitats, extensions of range, uses by the inhabitants, and numerous other details will make it valuable to both the botanist and the anthro-

poligist. The original approach reflected in the way the book is written is refreshing and gives point to the admonition, often heard but perhaps too infrequently heeded, that every naturalist should spend MONTHS in the field before attempting to write about his observations. The 23 months Mr. Gentry spent in the Rio Mayo region certainly paid dividends in botanical data.—IRA L. WIGGINS, Stanford University.

PRACTICAL PLANT ANATOMY. By Adriance S. Foster. D. Van Nostrand Company, New York, 1942. x + 155 pp., flexible cover, spiral binding. \$2.50.

Plant anatomy has had a rather long history and considerable knowledge has been accumulated during that time. However, real progress regarding certain crucial problems has been made only in recent years, especially with reference to the structure of the cell wall, the cytoplasm and its inclusions, meristems etc. A completely satisfactory classification of plant cell types and tissues has not yet been proposed and, in the opinion of some, can not be proposed until our knowledge of the physiological characteristics of the protoplast is such that the classification of tissues can ultimately be based on the living constituents of the plant cell rather than on the dead cell walls as in the past.

Although this manual is intended to serve as a guide for laboratory use, it goes far beyond the available textbooks in presenting clear and concise summaries of the significant newer knowledge of plant anatomy. Sound and ample laboratory exercises and directions, frequently using economic plants as types, are found in the fourteen chapters which cover the protoplast, the major cell types and tissues, and the principal vegetative organs. Especially well prepared are chapter III on meristems and chapter IV dealing with problems on the classification of cell types, tissues and tissue systems in vascular plants including a very useful tabular summary of the main cell types in seed plants. This classification is admittedly non-committal and incomplete, since it is designed for practical purposes and does not treat of reproductive structures and highly specialized secretory and sensory cells. For the benefit of the reader each chapter is accompanied by a list of references, most of which are of very recent date.

Practical Plant Anatomy is thus not only a very excellent laboratory manual but also a splendid introduction to the ramified and often controversial literature of the field, which is treated in a remarkably objective manner. The book is the outgrowth of the author's research and long experience in teaching plant anatomy. Fully aware of the diversity of possible course work and material, the author has wisely absolved himself of such chapters as would be necessary to treat microchemical reagents, the gametophyte etc., and has rightly placed the emphasis on the sporophyte. No criticism, then, is levelled at the author for his selection of subject matter, material, and instructions. This reviewer merely wonders about the possibility of including in a book of this kind a short chapter on the tissues of fossil plants. Few courses in anatomy seem to consider them despite their great phylogenetic importance and practical value not only for paleobotanical studies but also for ethnobotany, dendrochronology, wood anatomy etc. (see Elise Hofmann, *Paläohistologie der Pflanze*, Vienna, 1934). Since most modern classifications of the vascular plants are based largely on the structure of the vegetative plant rather than on that of the gametophyte, the above suggestion is apparently in keeping with this viewpoint, even if it would require a mild departure from accepted practice.—THEO. JUST.



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